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Date of this issue 6 May 1988

Organisms of a Subtidal Sand Community in Southern California

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Abstract. — A long-term study of a subtidal sand community on the exposed coast of California has revealed a highly structured, diverse assemblage of macroscopic, epifaunal organisms. It is dominated by a few species of relatively large, long-lived suspension feeders, particularly the sand dollar *Dendraster excentricus*. Along the depth gradient from 2.6 m to 13.1 m there are three faunal zones with the sand dollars occupying most of the middle zone. The community is composed of about 45 common species; the seaward zone has the greatest diversity and number of predators. Nearly 90 invertebrate and more than 30 fish species were recorded during the study.

The subtidal nearshore regions of the southern California coastline are dominated by long stretches of uninterrupted sand bottoms. Within these habitats there often occur immense beds of the sand dollar *Dendraster excentricus*. The distribution of these beds has been documented in detail by Merrill and Hobson (1970) and also discussed by others (Parks 1973; Dexter 1978; Cameron and Rumrill 1982). The dynamics of these beds have been extensively studied by Morin et al. (1985). The general organization of soft-substrate communities in southern California has also been addressed by Fager (1968), Davis and VanBlaricom (1978), Oliver et al. (1980), Kastendiek (1982), and VanBlaricom (1982).

Despite the unstable, dynamically changing nature of the substrate that occurs in the shallow sandy subtidal, the associated animal assemblages tend to be highly structured and show complex interactions between the physical and biological components of the environment (Morin et al. 1985). The present paper provides a thorough documentation of the macroscopic epifauna and some of the infauna that regularly occur in and around a representative sand dollar bed in southern California.

Methods

The observations presented here were collected from March 1970 to January 1975 by scuba diving at a variety of locations along Zuma Beach (118°50'W, 34°01'N), 35 km northwest of Los Angeles, California. However, most of the data were collected from two transects located 0.4 km apart and ranging in depth from

2.6 m (MLLW) and 13.1 m (Morin et al. 1985). Each transect was permanently marked at its ends by stakes placed 180 m apart along the bottom and perpendicular to shore. One transect was displaced 30 m seaward relative to the other so that the combined transect length was 210 m. Censuses of macroscopic epifauna (>5 mm) and visible infauna were accomplished by counting individuals within a one-meter wide path along each five-meter interval of a polypropylene line that was attached to the stakes just before each census. Sand dollar densities were determined from counts of individuals found within a 0.1 m² ring blindly tossed at regular intervals along the transect. Less abundant organisms were censused from counts of transects that were 10 m wide along the entire distance of 180 m. The observations reported here are derived from 65 complete transects, 28 partial transects, and a total of 208 dives encompassing about 554 person-hours of underwater surveying. Other details of our methods are reported in Morin et al. (1985).

Results

The subtidal sand bottom off Zuma Beach is divisible into three distinct zones (Fig. 1): (1) the shoreward zone (2.6–6.4 m depth [MLLW]), which is dominated by the Pismo clam *Tivela stultorum* and the sea pansy *Renilla kollikeri*, (2) the middle or sand-dollar zone (6.4–9.1 m depth [MLLW]), which is dominated by the sand dollar *Dendraster excentricus*, and (3) the seaward zone (9.1–13.1 m depth [MLLW]), which is dominated by the sea pen *Stylatula elongata*, the sea pansy *Renilla kollikeri*, the sea star *Astropecten armatus*, and the tube worm *Diopatra ornata* (see also Morin et al. 1985). Nearly 90 macroscopic invertebrate species and over 30 fish species were encountered during the study (Table 1). Detailed information on the distributions, frequencies and abundances, relative locations, and particular features of all these organisms is given in Table 1.

Discussion

The shallow subtidal sand habitat at Zuma Beach in southern California is composed of a rich assemblage of epifaunal organisms capable of survival in shifting sediments and buffeting sands. Among all the organisms we encountered during our study, over two-thirds were permanent, resident sand dwellers, and about one-quarter were transients from distant rocky habitats; the remainder occur in both types of habitats. Similar to reports of most rocky subtidal habitats (e.g., Pequegnat 1968), the sand community at Zuma Beach is dominated, in both numbers and biomass, by suspension feeding organisms, particularly *Dendraster excentricus*, *Renilla kollikeri*, *Stylatula elongata*, and *Tivela stultorum* (Table 1 and Morin et al. 1985). All of these species are relatively large, long-lived suspension feeders and thus represent an enormous permanent standing crop that is relatively stable, but with low rates of turnover and productivity (Morin et al. 1985). Because of the instability of the substrate, attached plants, and hence herbivores, are virtually absent from this habitat. Carnivores, however, are common but occur in relatively low densities, and fall into two major categories: highly motile species and creepers. Highly motile carnivores (e.g., the decapods *Cancer gracilis*, *Randallia ornata*; the fishes *Citharichthys stigmaeus*, *Pleuronichthys coenosus*, *Hypsopsetta guttulata*) can tolerate substantial surge and thus occur throughout all zones (Table 1). It is only in the relatively calm seaward zone (at

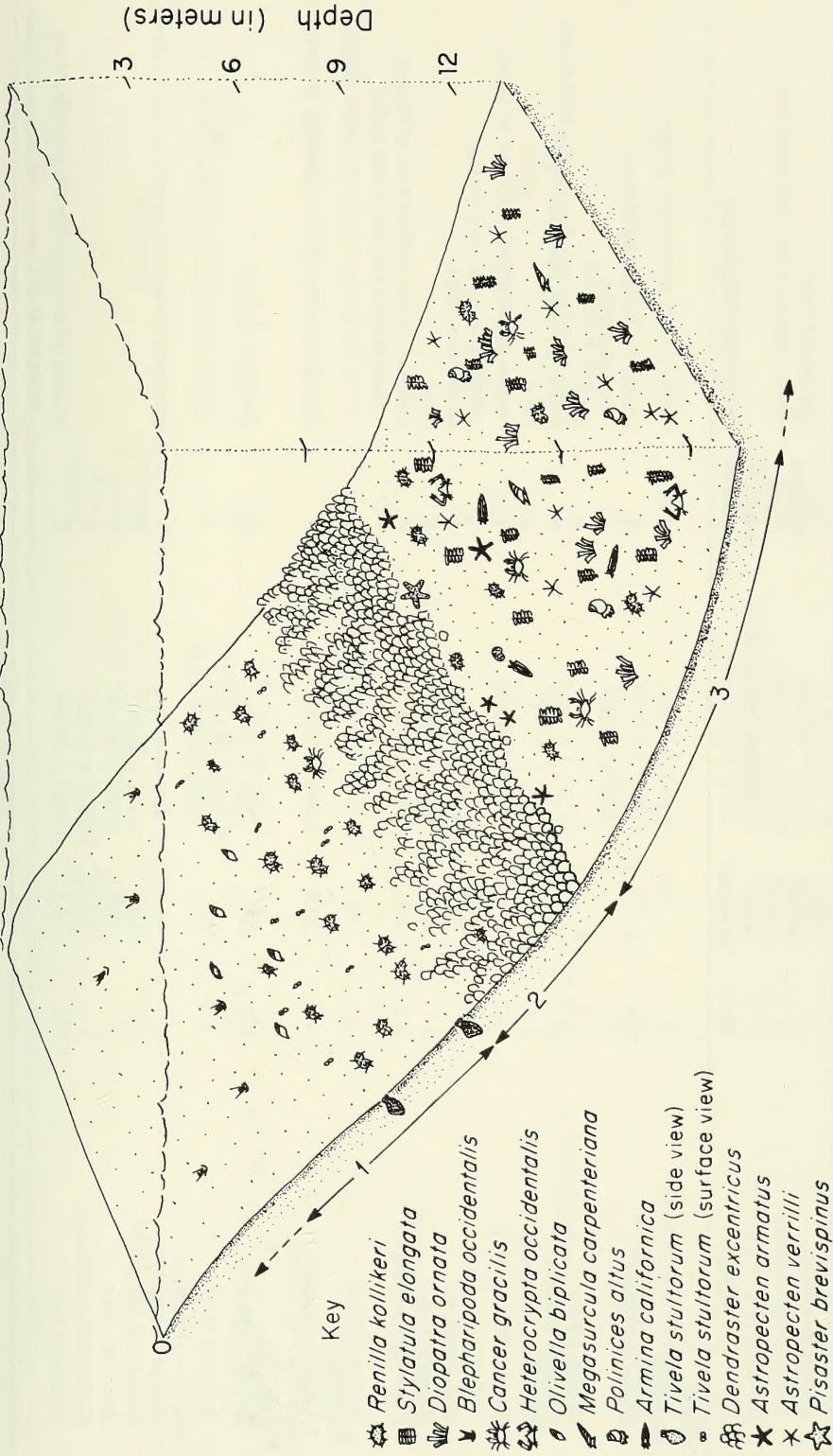


Fig. 1. Stylized section of the shallow subtidal sand bottom off Zuma Beach, California showing 15 of the common species from the three main biological zones (fishes not shown). Vertical scale is exaggerated.

Table 1. Characteristics of the macrofauna recorded within the study site at Zuma Beach.

Species ^{a,b}	Zone ^c	Per- centage of dives seen ^d (daytime)	Number seen per dive ($\bar{x} \pm \text{s.e.m.}$) ^e	Position with respect to substrate ^f	Comments
Cnidaria					
Hydrozoa					
<i>Obelia longissima</i>	2, 3	F	$4.94 \pm 0.316^{\Delta 1}$	A	usually on <i>Balanus pacificus</i> or <i>Diopatra</i> tubes
<i>O. dichotoma</i>	2, 3	F		A	same
<i>Lovenella producta</i>	2	F		A'	usually on dead <i>Dendroaster</i> tests
<i>Campanulina rugosa</i>	2	F	$4.88 \pm 0.919^{\Delta 2}$	A'	same
<i>Clytia bakeri</i>	1, 2	F	$2.87 \pm 0.275^{\Delta 3}$	A'	usually on live <i>Olivella biplicata</i> or <i>Tivela</i> shells
<i>Aglaophenia</i> sp.	3	7.4	0.0750 ± 0.0209	A'	on <i>Diopatra</i> tubes
<i>Plumularia</i> sp.	3	4.1	0.0438 ± 0.0162	A	same
<i>Polyorchis penicillatus</i>	3, 2	4.7	0.0663 ± 0.0228	P	medusae usually within 10 cm of bottom more often in the winter and spring
Scyphozoa					
<i>Pelagia colorata</i> †*	—	10.8	0.590 ± 0.144	P	throughout water column especially in spring
Anthozoa					
<i>Renilla kollikeri</i> * ^x	1, 2, 3	100	$226 \pm 21.0^{\Delta}$ (summer: 211 ± 33.3 winter: 218 ± 43.3)	S	dominant species
<i>Stylatula elongata</i> * ^x	3	96.6	$40.4 \pm 4.03^{\Delta}$	S	dominant species
<i>Harenactis attenuata</i> * ^x	3, 2	18.1	0.181 ± 0.0415	S'	
<i>Zaolutus actus</i>	3	10.8	0.163 ± 0.0406	S'	
<i>Edwardsiella californica</i>	3	4.7	0.0625 ± 0.0211	S'	
<i>Halacampa</i> sp.‡	3, 2	4.1	0.0750 ± 0.0244	S	extends off substrate like <i>Corymorpha</i> , most common in fall

Table 1. Continued.

Species ^{a,b}	Zone ^c	Per-centage of dives seen ^d (daytime)	Number seen per dive ($\bar{x} \pm \text{s.e.m.}$) ^e	Position with respect to substrate ^f	Comments
Annelida—Polychaeta					
<i>Diopatra ornata</i>	B, 3, 2	100	342 $\pm$ 41.2 ^{a,4}	S	tubes extend several cm above sand
Cirratulidae	2, 1, 3	13.5	0.193 $\pm$ 0.0498	S'	
Sabellidae	3	5.4	0.0843 $\pm$ 0.0376	S'	
Arthropoda—Crustacea					
Cirripedia					
<i>Balanus pacificus</i>	2, 1	100	[0.0351 $\pm$ 0.00703/100 D.e.] ^{a,5}	A	mostly on <i>Dendraster</i> but also other exposed hard substrates
Malacostraca—Decapoda					
Caridea					
<i>Heptacarpus</i> sp.	2	F (8.1)	—	E	common between sand dollars nocturnally active
<i>Crangon nigricauda</i> *	—	2.7*	0.027 $\pm$ 0.0124	I (E)	
Anomura					
<i>Isocheles</i> (= <i>Holopagurus</i>) <i>pilosus</i>	2, 3, 1	27.0	0.296 $\pm$ 0.0431 ^a	E	more common near the seaward edge of the sand dollar bed
<i>Paguristes bakeri</i>	3	4.1	0.0675 $\pm$ 0.0298	E	
<i>Pagurus spillocarpus</i> (?)	3	4.1	0.0405 $\pm$ 0.0134	E	
<i>Blepharipoda occidentalis</i>	S, 1	3.4*	0.0875 $\pm$ 0.0535	I (S')	appears to be more active at night
Brachyura					
<i>Cancer gracilis</i> **	—	37.2*	0.478 $\pm$ 0.150 ^a	I (E)	nocturnally active
<i>Heterocrypta occidentalis</i> *	3, 2	33.8	0.846 $\pm$ 0.171 ^a	E to S'	
<i>Loxorhynchus grandis</i>	2, 3, 1	33.1	0.0986 $\pm$ 0.0409 ^a	E	most common in the sand dollar bed
<i>Randallia ornata</i> **	—	25.7*	0.152 $\pm$ 0.0436 ^a	I (E)	nocturnally active
<i>Cancer antennarius</i> †*	—	15.5	0.194 $\pm$ 0.0371	E	
<i>C. productus</i>	—	10.1	0.119 $\pm$ 0.143	E	
<i>C. anthonyi</i>	—	6.8	0.0811 $\pm$ 0.0269	E	
<i>Portunus xantusii</i>	—	5.6*	0.0563 $\pm$ 0.0275	I (E)	more common at night, nocturnally active

Table 1. Continued.

Species ^{a,b}	Zone ^c	Per- centage of dives seen ^d (daytime)	Number seen per dive ($\bar{x} \pm \text{s.e.m.}$) ^e	Position with respect to substrate ^f	Comments
Mollusca					
Pelecypoda (Bivalvia)					
<i>Tivela stultorum</i>	1	99.3	2.61 $\pm$ 0.791 ^o	S'	usually only siphons show, dominant species
<i>Clinocardium nuttallii</i>	2, 3	10.2	0.102 $\pm$ 0.0265	S'	
<i>Donax gouldii</i>	S, 1	4.8	0.0479 $\pm$ 0.0166	S'	near surf zone
Gastropoda					
<i>Armina californica</i> †*	3, 1, 2	68.2	8.34 $\pm$ 1.22 ^o	E to S	
<i>Polinices altus</i>	3, 2	45.9	1.53 $\pm$ 0.252 ^o	S' to E	most common in the fall and winter
<i>Megasurcula carpenteriana</i>	3, 2	43.2	0.917 $\pm$ 0.115 ^o	E	
<i>Olivella biplicata</i>	1, S	39.9	1.47 $\pm$ 0.328 ^o	S'	
<i>Balcis rutila</i> †	2, 3	37.8	[17.99 $\pm$ 2.55/100 D.e.] ^{a,6}	E or A	usually found ectoparasitic on <i>Dendraster</i> , most common in the summer
<i>B. micans</i>	3, 2	I*	—	I to E	ectoparasitic on echinoderms or free living on sand
<i>Terebra pedroana</i> *	3	16.2	0.302 $\pm$ 0.0418	E	
<i>Nassarius fossatus</i>	2, 3	13.5	0.144 $\pm$ 0.0331	S' to E	
<i>Ophiodermella ophioderma</i>	3	10.8	0.278 $\pm$ 0.0662	E	
<i>Rictaxis</i> (= <i>Acteon</i>) <i>punctocaelatus</i>	3, 2	8.1	0.0964 $\pm$ 0.0342	S' to E	
<i>Hermisenda crassicornis</i> †	3	6.8	0.192 $\pm$ 0.0550	A or E	on <i>Diopatra</i> tubes with hydroids especially during the summer
<i>Kelletia kelletii</i> †	3	7.4	0.0867 $\pm$ 0.0244	E	
<i>Olivella baetica</i>	3, 2	7.4*	0.125 $\pm$ 0.0467	S' to I	
<i>Polinices lewisii</i>	3, 2	5.4	0.0542 $\pm$ 0.0176	E	
<i>Mitra idae</i> †	3	3.4	0.0500 $\pm$ 0.0247	E	
<i>Nassarius perpinquis</i>	3	2.0*	0.0361 $\pm$ 0.0211	I to S'	
<i>Cuthona divae</i> †	3, 2	2.7	0.0349 $\pm$ 0.0182	A or E	on <i>Diopatra</i> tubes in winter
<i>Coryphella trilineata</i> †	3	1.4	0.0174 $\pm$ 0.0099	A or E	same

Table 1. Continued.

Species ^{a,b}	Zone ^c	Per-centage of dives seen ^d (daytime)	Number seen per dive ($\bar{x} \pm \text{s.e.m.}$) ^e	Position with respect to substrate ^f	Comments
Echinodermata					
Echinoidea					
<i>Dendraster excentricus</i> ^x	2, 3	100	18,300 $\pm$ 597 ^{Δ7}	S or E	dominant species
<i>D. laevis</i>	3, B	3.4	0.0375 $\pm$ 0.0320	S	
Holothuroidea					
<i>Molpadia arenicola</i>	2, 3	33.1*	0.466 $\pm$ 0.0645 ^x	I to S'	
Ophiuroidea					
<i>Amphiodia occidentalis</i> ^{†x}	3, 2	14.2*	0.690 $\pm$ 0.127	S'	arms extend several cm above sand, mostly in the fall
Asteroidea					
<i>Astropecten verilli</i>	B, 3	98.6	17.4 $\pm$ 3.46 ^o	E to I	dominant species
<i>A. armatus</i> (= <i>braziliensis</i>)	2, 3	97.3	2.19 $\pm$ 0.209 ^o	E to I	dominant species
<i>Luidia</i> (= <i>Petalaster foliolata</i>) [†]	3	31.1	0.535 $\pm$ 0.113 ^o	E to I	most prevalent in spring
<i>Pisaster brevispinus</i>	2, 3, 1	29.7	0.0725 $\pm$ 0.0376 ^o	E	
<i>P. giganteus</i>	2, 3, 1	29.1	0.145 $\pm$ 0.0427 ^o	E	
<i>Patiria miniata</i> [†]	2, 3	8.8	0.109 $\pm$ 0.0299	E	most common in fall
Chordata — Vertebrata					
Chondrichthyes					
<i>Platyrrhinoidis triseriata</i> [*]	—	15.5*	0.179 $\pm$ 0.0337	I (E)	nocturnally active
<i>Myliobatis californica</i>	—	10.1	0.101 $\pm$ 0.0239	E	
<i>Torpedo californica</i>	—	10.1	0.101 $\pm$ 0.0226	E to S	
<i>Rhinobatos productus</i>	—	2.7	0.0447 $\pm$ 0.0155	E to S	
Osteichthyes					
<i>Citharichthys stigmaeus</i>	—	99.3	1.07 $\pm$ 0.236 ^o	E	dominant species
<i>Pleuronichthys coenosus</i>	—	42.3	0.479 $\pm$ 0.0918 ^o	E to S	

Table 1. Continued.

Species ^{a,b}	Zone ^c	Per- centage of dives seen ^d (daytime)	Number seen per dive ($\bar{x} \pm \text{s.e.m.}$) ^e	Position with respect to substrate ^f	Comments
<i>Hypsopsetta guttulata</i>	—	31.8	0.260 $\pm$ 0.0618 ^o	E to S	
<i>Paralichthys californicus</i>	—	22.3	0.0960 $\pm$ 0.0346 ^o	E to S'	more common in summer than fall
<i>Paralabrax clathratus</i>	—	12.9	0.541 $\pm$ 0.118	P	
<i>Synodus lucioceps</i>	3, 2, 1	8.8	0.134 $\pm$ 0.0706	E	more common in summer
<i>Menticirrhus undulatus</i>	S	8.1	0.0811 $\pm$ 0.0745	P	near surf line
<i>Phanerodon furcatus</i>	—	7.4	0.138 $\pm$ 0.0496	P	
<i>Hyperprosopon argenteum</i> *	S	6.8	0.206 $\pm$ 0.0860	P	near surf line by day, throughout by night
<i>Damalichthys vacca</i>	—	4.7	0.0938 $\pm$ 0.0464	P	

^a Includes all macroscopic (> 5 mm) epifauna and partially visible infauna detected on more than 2% of the dives within the study area.

^b ‡ = Seasonally abundant (see also table 1 in Morin et al. 1985).

* = Nocturnally active (see also table 2 in Morin et al. 1985).

× = Indicates long term (4 year) population variations (see also table 3 in Morin et al. 1985).

+ = Transient, most common in rock and kelp habitats.

^b Rare species (encountered on <2% of the dives) and includes, in order within the parentheses: the zone of occurrence (see c), position with respect to the substrate (see f), and, if available, the no. seen per dive $\pm$ s.e.m. (see e); * = nocturnally active: Cnidaria, Hydrozoa: *Bougainvillea* sp. (3, A), *Tubularia* sp. (3, A), Anthozoa: *Virgularia bromleyi* (B&3, S); *Epiactis prolifera* (3, A); Annelida, Polychaeta: *Aphrodita* sp. (3, I), Terebellidae (3, S'); Arthropoda, Palinura: *Panulirus interruptus* (2, E), Anomura: *Emerita analoga* (S, S'), Brachyura: *Podochela hemphillii* (3, E), *Talipes nuttallii* (3, E), *Mursia quadricaudii* (B, E), *Pugettia richii* (2, E); Mollusca, Gastropoda: *Coryphella cooperi* (3, A or E), *Polycera atra* (3, A or E), *Cancellaria cooperi* (B, E), *Epitonium* sp. (3, S' to E), *Tritonia exulans* (B, E), *Aplysia californica* (3, E), Cephalopoda: *Octopus bimaculatus* (2, E; 0.014 $\pm$ 0.009); Brachiopoda: *Glottidia albida* (3, D); Echinodermata, Echinoidea: *Lovenia cordiformis* (3, I), Holothuroidea: *Leptosynapta* sp. (3, I), Asteroidea: *Pisaster ochraceus* (2, E); Chordata, Chondrichthyes: *Squatina californica* (—, E to S; 0.020 $\pm$ 0.002), *Urolophus halleri* (1, E to S), *Triakis semifasciata* (—, E to P), *Cephaloscyllium ventriosum* (—, E to P), Osteichthyes: *Xystreurys liolepis* (B&3, E to S; 0.027 $\pm$ 0.014), *Amphistichius argenteus* (S, P), *Leptocottus armatus** (—, 1 but E at night), *Neoclinus blanchardi* (—, E; 0.019 $\pm$ 0.011), *Chilara taylori** (—, 1 but E at night), *Scorpaena guttata* (—, 1 but E at night; 0.026 $\pm$ 0.013), *Scorpaenichthys marmoratus* (—, E), *Syngnathus* sp. (—, E), *Hippoglossina stomata* (B&3, E to S), *Parophrys vetulus* (B&3, E to S), *Pleuronichthys ritteri* (B&3, E to S), *P. verticalis* (B&3, E to S), *Porichthys notatus* (B&3, S' to E), *P. myriaster* (B&3, S' to E).

^c Zones where the species have been observed are listed in their order of greatest to least encounters:

S = Shoreward of Zone 1 on the transect; <2.6 m depth.

1 = Zone 1; 2.6 to 6.5 m depth (0–55 m on the transect).

2 = Zone 2; 6.5 to 9 m depth (55–100 m on the transect).

3 = Zone 3; 9 to 13 m depth (100–210 m on the transect).

Table 1. Continued.

B	= Beyond the transect to the seaward; > 13 m depth.
—	= Not clearly restricted; occurs in all zones (1–3); 2.6 to 13 m depth.
^a	Percentages are taken from about 148 dives and give an indication of the number of zeros involved in the number seen per dive.
F	= Frequently encountered (> 50%) but often not noted in dive logs.
*	= Infaunal or barely exposed during the day so that the abundance is probably underestimated.
I	= Intermittently observed and usually not recorded in dive logs.
^e	Numbers are the averages of about 148 dives except for species seen > 20% of the time (see also Figs. 3 and 8 in Morin et al. 1985) and are from:
□	= numbers observed during transects only (65)
△	= numbers observed during special censuses:
1.	<i>Obelia</i> spp. combined: 70 censuses; species indistinguishable in the field.
2.	<i>Lovenella</i> and <i>Campanulina</i> (f. Campanulinidae) combined: 17 censuses; genera indistinguishable in the field.
3.	<i>Clytia bakeri</i> : 22 censuses.
4.	<i>Diopatra ornata</i> : 10 censuses; N = 354 in the Feb. 1971 census and 620 in Feb. 1974 (see also fig. 3 in Morin et al. 1985).
5.	<i>Balanus pacificus</i> : 9 censuses and expressed as the number of barnacles attached per 100 <i>Dendroaster</i> (<i>D.e.</i>) examined (see also fig. 3 in Morin et al. 1985).
6.	<i>Balcis rutila</i> : 37 censuses and expressed as the number of barnacles attached per 100 <i>Dendroaster</i> (<i>D.e.</i>) examined (see also fig. 8 in Morin et al. 1985).
7.	<i>Dendroaster excentricus</i> : 62 censuses.
x	= calculated on basis of 148 dives.
*	= too infrequent to calculate.
r	A = Epifaunal and attached to a solid substrate.
A'	= Same, but solid substrate may be partially buried in sand.
P	= Pelagic; swimming; not normally resting.
E	= Epifaunal; resting on the substrate.
S	= Substrate associated but being mostly exposed but also partly buried or anchored in the sand.
S'	= Substrate associated but being mostly buried or anchored in the sand and with only a limited amount of the organism exposed.
I	= Infaunal; usually not exposed or visible from above the substrate.
()	= Position of the species at night in the nocturnally active forms.

depths >9.1 m), where sand movement and surge become negligible, that creeping carnivores and scavengers (e.g., the asteroids *Astropecten verrilli*, *Luidia foliolata*; the gastropods *Armina californica*, *Polinices altus*, *Megasurcula carpenteriana*) become common (Table 1). Thus, this deeper zone also has the greatest number of species.

Merrill and Hobson (1970) made an extensive survey of sand dollar beds along the coast of western North America from Eureka, California south to Bahia de Todos Santos, Baja California, Mexico. From sand habitats south of Point Conception, California they reported about 53 species of organisms associated with sand dollar populations from the outer-coast (Merrill and Hobson 1970—table 4, p. 613). Of these 53 species, we recorded about three-quarters (38 species) within our study area at Zuma Beach. We have, however, observed all of the other 15 species in other locations either near the ends of the 6 km-long sand dollar bed at Zuma Beach or at nearby locations. Furthermore, 10 of the 15 are listed by Merrill and Hobson as occurring only in some beds and surrounding areas; thus they may be rare or absent within our study area. The differences between the two studies are probably due to: 1) fluctuations in the population densities between the two study periods, 2) differences in habitats (Merrill and Hobson studied a much broader range of habitats and bottom configurations while the habitat in the present study was much more homogeneous), and 3) some infaunal organisms not being systematically sampled in either study. In addition, misidentification is always a possibility.

The combined species numbers from Merrill and Hobson (1970) and our study (see also Morin et al. 1985) yields a very large, diverse macrofauna of over 135 species that live on or near these subtidal sand surfaces. And this list does not include the rich and diverse (although low biomass) infaunal and meiofaunal populations that occur in these kinds of habitats (Dexter 1978; Smith 1981; VanBlaricom 1982). From all of these studies it is clear that southern California subtidal sand habitats contain a highly structured, zonally organized community, dominated by specialized organisms whose populations are dynamically modulated through complex interactions with the physical environment and with one another.

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Foraging Patterns of Yellowjackets, *Vespula pensylvanica*, in an Artificial Flower Patch

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Abstract. — *Vespula pensylvanica*, yellowjackets, were attracted to artificial flower patches, made repeated foraging trips, and returned on successive days. We observed the foraging patterns of *Vespula pensylvanica* in blue-yellow color-dimorphic and clove-peppermint odor-dimorphic artificial flower patches, with variable sucrose molarities and volumes, as previously used to study honey bees. Yellowjackets foraged randomly in color-dimorphic patches regardless of reward volume or odor. When one morph provided 1.5 M sucrose, the other 2.5 M sucrose, vespid wasps foraged randomly. When one morph provided 1.5 M sucrose, and the other flower morph 0.75 M sucrose, yellowjackets visited randomly but only drank the richer solution. In odor-dimorphic monochromatic patches yellowjackets foraged randomly.

Introduction

Vespid wasps, like honey bees and bumble bees, are social hymenopterans. Their diets are more diverse than those of bees, but often include nectar gathered from flowers (Akre et al. 1980; Ross 1983). In fact, when studying foraging patterns of honey bees (Wells et al. 1981, 1983; Wells and Wells 1983, 1984, 1985, 1986), vespid wasps (yellowjackets), often ventured into the artificial flower patches and foraged there for extended periods. This led to the systematic observation of yellowjacket foraging patterns in color- or odor-dimorphic artificial flower patches under conditions comparable to those used to study honey bees.

Experiments were designed to compare yellowjacket foraging to that of honey bees by testing the null hypotheses of random visitation to flower morphs by vespid wasp foragers, uniform visitation (all foragers exhibit similar behavior) by yellowjacket foragers, and unchanging behavior by individual yellowjackets under the following conditions: 1) each flower, blue and yellow, provided a full load of scented sucrose solution; 2) each flower presented a smaller volume of reward so that a yellowjacket had to visit many flowers per trip from the nest to harvest a full load of scented sucrose solution; 3) unscented rewards were provided in both colors of a dimorphic flower patch; 4) flowers were provided that were odor-dimorphic and monochromatic; 5) one color flower had a higher quality reward than the other color flower in a dimorphic flower patch.

Methods

Yellowjackets, *Vespula pensylvanica*, were studied at Switzer's Picnic Area in the Angeles National Forest 35 km north of Occidental College, Los Angeles, on

Highway 2. Yellowjackets which had been scavaging at the picnic area readily began to forage on the artificial flower patch. Each yellowjacket involved in the experiment was given an individually recognizable paint dot on its thorax or abdomen. The yellowjackets were not traced to their nests, therefore, they may not have all come from a single colony.

Foraging patterns of yellowjackets harvesting sucrose solution from an artificial flower patch were recorded under five experimentally controlled conditions with $N \geq 5$ in each experiment. Observation periods were of two hours duration from 11:00 a.m. to 1:00 p.m., and were the only times we provided food or exposed the vespulid wasps to artificial flower patches.

The artificial flower patch used was of a previously published design (Wells et al. 1981). In that system a "flower" was defined as a piece of 6 mm clear plexiglass 30 mm square on a pedicel 90 mm long, with a 3 mm $\times$ 5 mm feeding well (a "nectary") in one corner of the upper surface. The bottom surface of each flower was painted with either No. 1208 blue or No. 1214 yellow Testors enamel. The grids used had 36 flowers, arranged on a brown background board in a Cartesian coordinate system. Flower colors or odors were arranged randomly by the use of a table of random numbers, and random arrangements were changed between and during experiments as a control for the possible use by vespulid wasps of flower position as a foraging cue. A modified pipette was used to dispense the sugar solution. Each flower and the background board were washed after each trial.

In the color-dimorphic flower patches equal numbers of blue and yellow flowers were randomly arranged to form a grid of 36 flowers, spaced at 75 mm. In the odor-dimorphic patches, thirty-six flowers were all of one color, spaced at 150 mm rather than 75 mm, and two different scents were randomly distributed among them, one scent per flower.

Chi-square statistics were used to test the null hypotheses of random visitation and uniform visitation. The General Exact Test (Wells and King 1980) was used to test for change in behavior of individual foragers.

Condition 1. Each blue or yellow flower provided a surplus of scented reward. Each of the 18 yellow and 18 blue flowers of a color-dimorphic flower patch was provisioned with 100 μ l of 1.25 M sucrose, scented at the rate of 200 μ ml/1 with oil of clove. Flowers were refilled after visitation by vespulid wasps, so that yellowjackets could obtain a full load by visiting only one flower per trip to the artificial flower patch. Yellowjackets were individually marked as they first visited the flower patch. Foraging patterns were recorded during two-hour observation periods on three successive days.

Condition 2. Each blue or yellow flower provided a smaller volume of scented reward so that yellowjackets visited several flowers on each trip from the hive in order to obtain a full load of nectar. On the day after the condition 1 experiments, the same set of yellowjackets was offered a flower patch in which each of the 18 blue and 18 yellow flowers was provisioned with 10 μ l of 1.25 M sucrose, scented at the rate of 200 μ l/1 with oil of clove. Flowers were refilled after visitation by wasps. Foraging patterns were recorded during a two-hour observation period.

Condition 3. Unscented rewards were provided in a color-dimorphic flower patch. Each of 18 yellow and 18 blue flowers of a color-dimorphic flower patch was provided with 10 μ l of 1.25 M unscented sucrose solution. Flowers were

Table 1. *Vespula pensylvanica* visitation to artificial flower patches containing 100 μ l clove-scented (200 μ l/l) 1.25 M sucrose rewards in each of 18 blue (B) and 18 yellow (Y) randomly arranged flowers.

Yellow-jacket #	Day 1		Day 2		Day 3		Total	
	B	Y	B	Y	B	Y	B	Y
1	13	12	13	16	5	9	31	37
2	8	10	10	14	4	5	22	29
3	11	3	16	5	9	10	36	18
4	—	—	9	7	11	8	20	15
5	—	—	7	6	9	4	16	10
6	—	—	5	7	2	4	7	11
7	—	—	1	5	3	5	4	10
Total	32	25	61	60	43	45	136	130

refilled as emptied. A new set of yellowjackets (different from those observed under conditions 1 and 2) visited the flower patch during two-hour observation periods on two successive days. The wasps were individually marked upon first visit to the flower patch, and their choices of flowers recorded.

Condition 4. Two differently scented rewards were provided in a uniformly colored flower patch. Thirty-six blue flowers were provisioned with 100 μ l 1.25 M sucrose solution, 18 scented at the rate of 200 μ l/l with clove oil and 18 scented with 200 μ l/l oil of peppermint. The scented rewards were randomly distributed in the flower patch. A new set of yellowjackets (different from conditions 1, 2 or 3) was marked and foraging patterns recorded for each vespulid wasp during two-hour periods. Whenever flowers were depleted they were refilled with rewards of the original scent.

Condition 5. One color flower provided a higher quality reward than the other in a dimorphic flower patch. A final set of yellowjackets different from those observed in conditions 1, 2, 3 or 4 was marked and their foraging patterns recorded as they visited a patch of 18 blue and 18 yellow flowers. Yellow flowers were provisioned with 100 μ l 2.5 M and blue flowers with 100 μ l 1.5 M clove-scented sucrose solutions. Flowers were refilled as emptied. Foraging patterns were recorded during a two-hour observation period.

A second experiment was performed the next day, using the same set of vespulid wasps, with yellow flowers provisioned with 0.75 M and blue flowers with 1.5 M clove-scented sucrose solutions. Flowers were refilled as emptied. Foraging patterns were recorded during a two-hour observation period.

Results

Condition 1. Each blue or yellow flower provided a surplus of scented reward. Foraging patterns of yellowjackets in a color-dimorphic flower patch when each blue and each yellow flower provided a surplus of scented reward are shown in Table 1. Yellowjackets foraged homogeneously (day 1: $\chi^2 = 4.0$, $df = 2$, $P > 0.10$; day 2: $\chi^2 = 10.1$, $df = 6$, $P > 0.10$; day 3: $\chi^2 = 4.8$, $df = 6$, $P > 0.50$; thus n.s. any day), which is to say they all exhibited the same foraging behavior. Furthermore, flower visitation appeared to be random with respect to color (day 1: $\chi^2 = 4.8$, $df = 3$, $P > 0.10$; day 2: $\chi^2 = 10.1$, $df = 7$, $P > 0.10$; day 3: $\chi^2 = 4.9$, $df = 7$, $P > 0.50$; thus n.s. any day) and yellowjackets individually did not change behavior between days (GET: H_0 unchanged behavior, $P \geq 0.9$ in each case).

Table 2. *Vespula pensylvanica* visitation to artificial flower patches containing 10 µl clove-scented (200 µl/l) 1.25 M sucrose rewards in each of 18 blue (B) and 18 yellow (Y) randomly arranged flowers. Yellowjackets are the same as those in Table 1.

Yellowjacket #	B	Y	Total
1	16	9	25
2	7	13	20
3	13	16	29
4	11	10	21
5	15	7	22
6	7	9	16
7	15	13	28
Total	84	77	161

Yellowjackets sometimes visited more than one flower during a trip to the flower patch, even though each flower always provided a surplus of reward. Individuals were easily disturbed by movements of other foragers or by the observers, but after taking flight would return to another flower, not necessarily of the same color. All changes in color of flowers visited were recorded and are included in Table 1.

Condition 2. Each blue or yellow flower provided a small volume of scented reward. Foraging patterns of yellowjackets in a color-dimorphic flower patch in which each flower provided only 10 µl of scented reward are shown in Table 2. At this volume of reward per flower, yellowjackets visited several flowers during each trip to the flower patch ($\bar{x}$ = 5.6). Visitation again was random (χ^2 = 7.4, df = 7, P > 0.25; n.s.) with respect to color and wasps did not differ significantly in their behavior (χ^2 = 7.1, df = 6, P > 0.25; n.s.). Behavior can be seen to be unchanged from condition 1.

Condition 3. Unscented rewards were provided in a color-dimorphic flower patch. Foraging patterns of yellowjackets in a color-dimorphic flower patch with all flowers provisioned with a surplus of unscented reward are shown in Table 3. Yellowjackets did not forage homogeneously (χ^2 = 14.7, df = 4, P < 0.01) when under condition 3. However, individuals 1, 3, 4 and 5 foraged homogeneously (χ^2 = 0.93, df = 3, P > 0.75; n.s.) and randomly (χ^2 = 1.32, df = 4, P > 0.75; n.s.), whereas yellowjacket 2 exhibited a preference for blue flowers.

As in condition 1, wasps often visited more than one flower during a trip to the flower patch. All changes in color of flowers visited were recorded and are included in Table 3.

Table 3. *Vespula pensylvanica* visitation to artificial flower patches containing 100 µl unscented 1.25 M sucrose rewards in each of 18 blue (B) and 18 yellow (Y) randomly arranged flowers.

Yellowjacket #	B	Y	Total
1	15	14	29
2	25	4	29
3	7	11	18
4	4	6	10
5	3	3	6
Total	54	38	92

Table 4. *Vespula pensylvanica* visitation to artificial flower patches containing 18 flowers with 100 μ l clove-scented (C) 1.25 M sucrose rewards, and 18 flowers with 100 μ l peppermint-scented (P) 1.25 M sucrose reward. Flowers were randomly arranged. All were blue.

Yellowjacket #	C	P	Total
1	9	10	19
2	8	3	11
3	8	11	19
4	3	7	10
5	5	5	10
Total	33	36	69

Condition 4. Two differently scented rewards were provided in a uniformly colored flower patch. Foraging patterns of yellowjackets visiting an odor-dimorphic monochromatic flower patch are recorded in Table 4. As in conditions 1 and 3 yellowjackets often visited more than one flower during a trip to the flower patch. All changes in odor of flowers visited are included in Table 4. Foragers were homogeneous in this behavior ($\chi^2 = 4.3$, $df = 4$, $P > 0.25$; n.s.), and visited flowers randomly with respect to scent ($\chi^2 = 4.4$, $df = 5$, $P > 0.50$; n.s.). Thus, yellowjacket foraging in an odor-dimorphic flower patch was identical to the general foraging behavior in the color-dimorphic experiments.

Condition 5. One color flower provided a higher quality reward than the other in a dimorphic flower patch. As in conditions 1, 3 and 4, foragers sometimes visited more than one flower during a trip to the flower patch. All changes in flower color visited were recorded and are included in Tables 5 and 6. When the blue flowers of a dimorphic patch provided 1.5 M and the yellow flowers 2.5 M clove-scented sucrose the foraging patterns recorded in Table 5 were observed. Yellowjacket foraging was both homogeneous ($\chi^2 = 2.8$, $df = 4$, $P > 0.50$; n.s.) and random ($\chi^2 = 2.8$, $df = 5$, $P > 0.50$; n.s.) with respect to color. Foragers visited and drank the rewards from both yellow (2.5 M reward) and blue (1.5 M reward) flowers.

When the blue flowers again were provided with 1.5 M and the yellow flowers 0.75 M of clove-scented sucrose, foraging patterns of these same yellowjackets were as shown in Table 6. Yellowjacket flower visitation was both homogeneous ($\chi^2 = 4.0$, $df = 4$, $P > 0.25$; n.s.) and random ($\chi^2 = 5.3$, $df = 5$, $P > 0.25$; n.s.) with respect to color. Foraging pattern was not quantitatively different from that recorded in Table 5.

Behavior of the yellowjackets in the last experiment (Table 6) was qualitatively different from that in all the other experiments. Only yellowjacket No. 3 (Table 6) drank the 0.75 M sucrose solution provided in the yellow flowers. The other yellowjackets tested it then moved to another flower (yellow or blue), drinking only when encountering the 1.5 M sucrose provided in the blue flowers. However, yellowjackets never learned not to test the flower color with lower molarity reward in either condition of experiment 5 (Tables 5 and 6).

Discussion

Yellowjacket nectar foraging appears to be significantly different from the behavior reported for honey bees under similar conditions. Honey bees when foraging on an artificial flower patch composed of pedicellate blue flowers and yellow

Table 5. *Vespula pensylvanica* visitation to artificial flower patches containing 18 blue (B) flowers with 100 μ l 1.5 M sucrose and 18 yellow (Y) flowers with 100 μ l 2.5 M sucrose reward. Flowers were randomly arranged and all rewards contained clove-scent (200 μ l/l).

Yellowjacket #	B	Y	Total
1	10	5	15
2	9	12	21
3	12	11	23
4	7	10	17
5	3	4	7
Total	41	42	83

flowers, randomly arranged, are each remarkably constant to one color or the other, but not all to the same color (Wells et al. 1981, 1983; Wells and Wells 1984). Honey bees are also individually constant to odor when two scents are randomly dispersed among uniformly colored pedicellate artificial flowers (Wells and Wells 1985). In these studies on honey bees, individually constant foraging in a patch of dimorphic pedicellate flowers persisted even when the flower morphs provided unequal qualities, volumes, or frequencies of reward. Individual constancy also persisted when distribution of morphs was patchy, rather than random (Wells et al. 1986).

Color-dimorphic flat flower patches which allow bees to walk, rather than fly from flower to flower, however, elicit a different behavior from honey bees. Individual honey bees foraged at random among alternative flower types when an artificial inflorescence had identical rewards in all flower morphs, and foraged optimally under conditions involving some reward differences (Waddington and Holden 1979; Wells and Wells 1984).

Bumble bees and wasps were reported to forage inclusively in artificial inflorescence-type flower patches (Real 1981). Foraging behavior of bumble bees on flat flower patches, like that of honey bees, is also variable. Inequalities of molarity and/or frequency of reward between morphs can result in "optimal diet" or "minimal uncertainty" patterns of foraging (Real 1981).

Complex flower patches, those involving three flower morphs (white, blue and yellow), demonstrated that, not only does honey bee foraging behavior vary in differing environments (Wells and Wells 1984), but that within a single flower patch individual bees foraged differently. Bees visited either both blue and white flowers, and foraged in an optimal diet manner between these two morphs, or

Table 6. *Vespula pensylvanica* visitation to artificial flower patches containing 18 blue (B) flowers with 100 μ l 1.5 M sucrose, and 18 yellow (Y) flowers with 100 μ l 0.75 M sucrose reward. Flowers were randomly arranged and all rewards contained clove-scent (100 μ l/l). Yellowjackets are the same as those in Table 5.

Yellowjacket #	B	Y	Total
1	13	5	18
2	8	10	18
3	16	10	26
4	8	8	16
5	5	6	11
Total	50	39	89

visited only yellow flowers. Those visiting blue and white rarely visited yellow, and those visiting yellow rarely visited blue or white flowers. Thus, individual constancy behavior acted as a superstructure, while optimal foraging occurred within subsets of flower morphs (Wells and Wells 1986).

Behavior of yellowjackets gathering nectar, on the other hand, did not involve individually constant foraging. Furthermore, yellowjackets often failed to take a full load of nectar from a flower when it was available. Finally, unlike bees, yellowjackets would not drink low molarity rewards (0.75 M) when encountered in a dimorphic pedicellate flower patch involving unequal rewards provided by the blue and yellow flowers. However, the yellowjackets did not learn to avoid a flower morph containing the lower molarity reward. Inability to distinguish the color difference between flower morphs does not appear to be the reason for continued visitation, without drinking the reward, to the lower reward-yielding flower morph. A yellowjacket in experiment 3, for example, did not forage randomly; rather, it predominantly visited blue flowers. Although not strictly optimal behavior, since foraging time was not minimized, yellowjackets did maximize caloric gain by drinking only the 1.5 M, not the 0.75 M sucrose solution in our second unequal quality experiment.

Evolutionary history differences may explain the differing foraging behaviors of yellowjackets and honey bees. Honey bees coevolved with angiosperms as primary pollinators (narrow diet). Yellowjackets evolved as predators and scavengers. The social structure of bees and wasps may be merely a convergent characteristic. Use of nectar, in fact, may be a relatively recent addition to the diets of socialized wasps so that little coevolution has occurred between species of yellowjackets and plants.

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Recruitment, Distribution, and Feeding Habits of Young-of-the-Year California Halibut (*Paralichthys californicus*) in the Vicinity of Alamitos Bay-Long Beach Harbor, California, 1983–1985¹

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Abstract.—Distribution, recruitment, and feeding habits of young-of-the-year (YOY, ≤ 80 mm SL) California halibut were investigated during the spring and early summer months of 1983–1985 in shallow water (0–6 m) near Alamitos Bay-Long Beach Harbor. YOY halibut were most abundant in fully-protected waters; semi-protected waters contained one-half to one-quarter the number of YOY halibut. No YOY halibut were collected at the exposed coast site.

Newly recruited halibut ranged from 8 to 12 mm SL and were approximately 20 to 29 days old. Gammarid amphipods, mysids, teleosts, and harpacticoid copepods were the major food items of YOY halibut. Recruitment was significantly greater in 1983 and 1984 than in 1985 (catch-per-unit-effort in 1983 > 1984 > 1985).

Introduction

The California halibut (*Paralichthys californicus*) is a major commercial and sport species in California. Commercial landings of halibut have steadily declined since recording began (Frey 1971). The commercial catch of halibut has declined since 1915, exhibiting progressively decreasing peaks in the 1930's, 1940's, 1960's, and early 1980's. Although the catch rose in 1981 (to 1.2 million pounds), it dropped off again in 1982 through 1984 (R. Collins, California Dept. of Fish and Game unpubl. data). Gill-netting pressure has increased (especially in southern California) over the last three to four years which may account, in part, for the slightly higher catches and subsequent decrease in landings. The "El Nino" event of 1982–1983 may also have had an impact on commercial catches through a northward shift in the distribution of adults. Catches from sport landings of California halibut showed a similar pattern to the commercial landings from the 1940's until about 1972 when the minimum size limit of 22 inches was put into effect. Thereafter, sport catch has remained very low. This trend may be best explained by the fact that sport boat fishing for halibut is no longer profitable and generally has been curtailed. The most probable explanations for the overall decline include over-exploitation of adult stocks by commercial fishing and destruction and alteration of nursery habitats (Plummer et al. 1983).

Although the actual status of the current halibut fishery is under debate, it seems clear that population levels are depressed relative to historical levels. Despite its

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historical importance to the commercial and sport fishery, until recently little has been known about the life history and ecology of California halibut. Frey (1971) summarized some of the information up to 1970 on the life history of California halibut. California halibut range from Long Beach, Washington to Magdalena Bay, Baja California with both the center of the commercial fishery and population center being from central California to northern Baja. Frey (1971) reported that halibut spawn in shallow water (9–20 m) from February to July. Halibut are relatively long-lived (up to 30 yr) females growing faster and attaining larger sizes than males. Males mature at about 2–3 years while females mature later at a much larger size (4–6 years). Some notable errors by Frey (1971) include the statement that halibut eggs are demersal and that settlement of juveniles occurs as early as June. Based on the information gathered since 1970, it is known that halibut eggs are planktonic like their larvae and settlement can occur as early as February. Additionally, the aforementioned depth range of spawning in California halibut may not be entirely correct and is currently being investigated using egg data (R. J. Lavenberg, LACMNH pers. comm.).

A study by Haaker (1975) presented information on younger stages of California halibut occupying the bay/estuarine environment of Anaheim Bay, California. He found that halibut in the year classes of 0 to 2+ primarily occupied the bay and presented information on growth, diet, movements, parasites, and some limited information on recruitment of YOY into the bay.

Plummer et al. (1983) presented valuable data on food habits in juvenile and adult halibut from open coast locations in the vicinity of San Onofre-Oceanside, California. These authors also summarized existing information on both the diet of halibut and on the habitats of the critical young-of-the-year (YOY) stage. They speculated that YOY halibut occur primarily in embayments along the California coast (see table 3, Plummer et al. 1983) and not in shallow coastal waters.

Reliable information on the spawning and the distribution of eggs and various larval stages of California halibut is only now becoming available. It has been known for some time that halibut spawn in nearshore, coastal waters primarily from February–July (Frey 1971; Gruber et al. 1982). However, the actual depth range of spawning is not known at this time. The planktonic eggs of halibut have recently been identified and information on their distribution within the nearshore waters should be forthcoming (R. Lavenberg pers. comm.). Halibut larvae were first described by Ahlstrom and Moser (1975) and have been recently distinguished (Ahlstrom et al. 1984) from the larvae of fantail sole (*Xystreurys liolepis*) within a limited size range. Planktonic larval stages (≤ 10 mm SL) occur throughout the water column, mainly over 12–45 m bottom depths within approximately 2–5.5 km of shore in the San Onofre-Oceanside region (Barnett et al. 1984 and unpubl. rep.). Larger larvae occur closer to shore. Halibut larvae are most abundant in the plankton in the San Onofre-Oceanside region during March–September (Barnett et al. 1984). Plummer et al. (1983) suggested that halibut larvae probably metamorphose in coastal water and migrate into embayments. The western Atlantic congener, *Paralichthys dentatus*, spawns offshore in coastal waters and larvae probably move into estuaries after metamorphosing nearshore (Smith and Daiber 1977). A similar species from the western Pacific, *Paralichthys olivaceus*, shows a similar pattern of life history in Japan (Minami 1982). Further, ichthyoplankton surveys of several bays and estuaries in southern California have shown

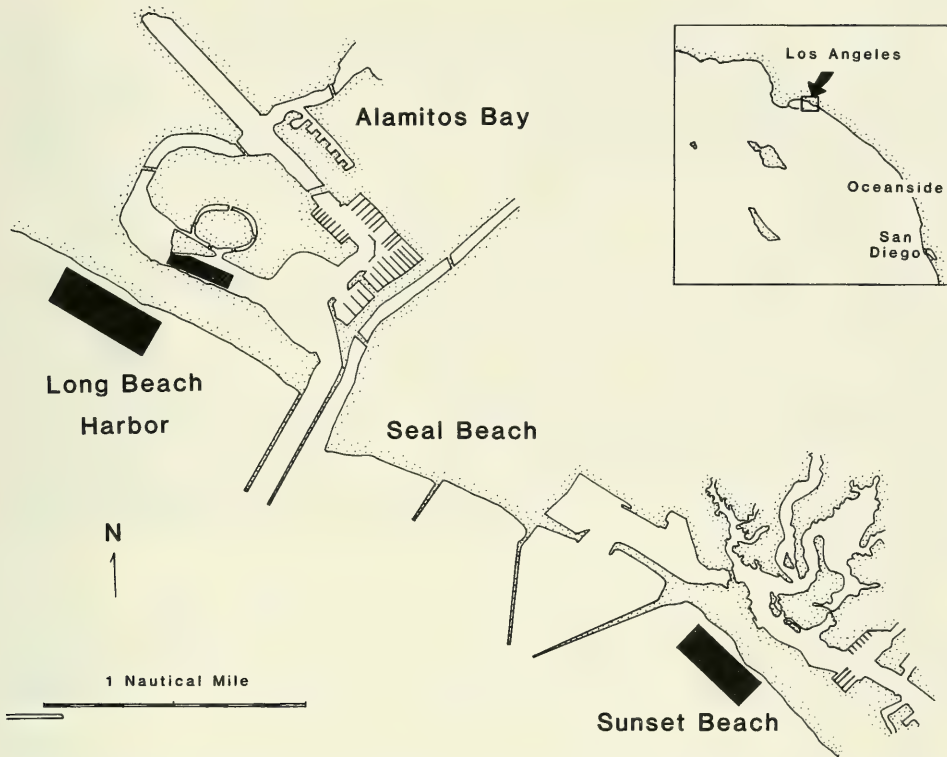


Fig. 1. Location of sampling stations within the study area near Alamitos Bay-Long Beach Harbor.

halibut larvae to be rare within the bays themselves (White 1977; Horn and Allen 1980; Leithiser 1981).

Although information on various aspects of the life history and ecology of California halibut is rapidly becoming available, little was known about the critical young-of-the-year stage prior to this study. This gap in information and the hypotheses about the distribution of early life history stages presented by previous authors (primarily Plummer et al. 1983) served as the impetus for the current study. The purpose of this paper is to present information on the young-of-the-year stage (≤ 80 mm SL) of the California halibut based on a three-year study (1983–1985) primarily in the area of Alamitos Bay-Long Beach Harbor, California. Specifically, this paper presents information on: 1) length frequencies and recruitment (i.e., settlement from the plankton) during 1983–1985; 2) estimated growth rates; 3) age-length relationships; 4) food habits; 5) patterns of distribution; and 6) recruitment success during the three years of the study.

Methods and Materials

Study Sites

Sampling was carried out primarily in the vicinity of Alamitos Bay-Long Beach Harbor in 1983–1985 (Fig. 1). Supplemental sampling was carried out in 1984 in the vicinity of San Onofre-Oceanside which served as a comparison site (Aqua Hedionda, near Carlsbad, California, Oceanside Harbor, and five open coast sites

10 km apart). At each location specific areas were ranked according to overall exposure to marine weather/swell influence. Embayment stations (Alamitos Bay and Aqua Hedionda) were designated as fully protected habitats. Long Beach and Oceanside harbors were designated as semi-protected habitats. Open coast sites were considered to be exposed habitats (Sunset Beach and five other sites from San Clemente to Oceanside).

Sampling Procedure

Sampling gear and effort varied over the three years of the study in an attempt to increase sampling efficiency and to satisfy the requirements of various funding agencies. In all three years, small seines were utilized to sample shore stations within Alamitos Bay. The seine used measured $4.9 \text{ m} \times 1 \text{ m}$ and consisted of 2 mm knotless, nylon mesh. In 1984, non-shore sampling was carried out using a 2 m beam trawl consisting of 2 mm knotless, nylon mesh. This method was found to have limited use in soft-substrate areas. Subsequently, in 1985, the non-shore stations were sampled with a 2 m otter trawl consisting of 4 mm mesh in the wings and 2 mm mesh in the bag. The otter trawl sampled effectively over all substrates encountered.

Seine samples from each of the three years of the study consisted of at least three replicates on each sampling date. The seine was hauled parallel to shore for 10 m and then pivoted straight onto the shoreline. This method of sampling covered approximately 65 m^2 per haul. A total of 78 seine hauls were made in the three years.

Otter trawl and beam trawl samples were deployed and retrieved in an identical manner. Five replicate, three minute tows were made randomly at each station with both the beam trawl (1984; $N = 45$) and the otter trawl (1985; $N = 105$) towed behind a 5 m Boston Whaler. The stations, as previously mentioned, corresponded to fully-protected, semi-protected, and exposed habitats at depths of 3–6 m. Beam trawl stations in the San Onofre-Oceanside area were sampled using an 8 m vessel (Raden).

Sampling in the Alamitos Bay region was carried out at approximately two-week intervals from 4 May to 27 July in 1983 (5 dates), 12 April to 20 June in 1984 (4 dates) and 13 March to 24 July in 1985 (8 dates). Supplemental sampling in the area of San Onofre-Oceanside was carried out on 13–15 June and 25 June 1984.

Surface temperature and salinity were recorded at each station using a Hydrolab sensing device, a bucket thermometer and an AO refractometer. Bottom temperature and salinity were recorded using the Hydrolab unit. All halibut caught in the seines or trawls were counted and measured alive on shore or on board the boat. In 1985, subsamples of at least ten individuals per date were either placed on ice for preliminary age determination or preserved in 10% formalin for later gut content analysis. Abundance of other fish and invertebrate species in the hauls was also noted.

In the laboratory, otoliths were dissected out and read using a light microscope. Growth rings were read in the sagittae of 10 individuals between 14 and 45 mm SL. We assumed that all rings represented daily growth checks.

Gut contents were examined for 67 individuals from the field subsamples which ranged in size from 7 to 77 mm SL. Digestive tracts were removed under a stereo-

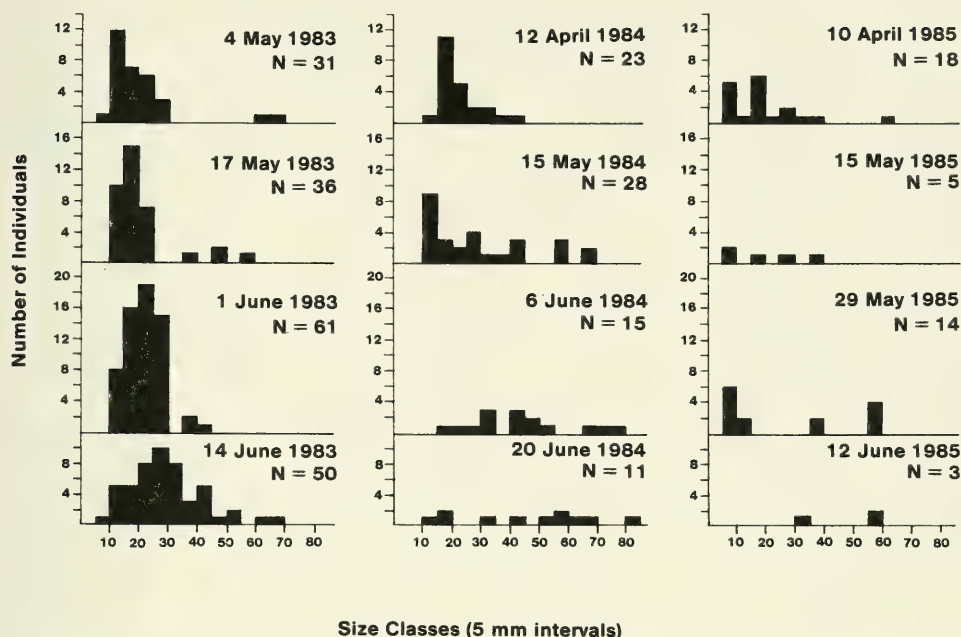


Fig. 2. Length frequency histograms for four comparable sampling dates in each year of the study, 1983–1985. Size classes are depicted in 5 mm intervals.

dissecting microscope, opened up, and the contents emptied into a petri dish. Items were identified to the lowest possible taxon and counted. The sorted items were then placed in aluminum pans, dried to a constant weight in a 50°C oven, and then weighed on an analytical Mettler balance to the nearest 0.001 g.

Statistical Procedures

Relative growth rates were determined for all three years by comparing the mean lengths of halibut for each sampling period. Age-length relationships were determined by least-squares linear regression. Gut content data were summarized as percent frequency of occurrence (F), percent number (N), percent dry-weight (W), and by calculation of the Index of Relative Importance. IRI (Pinkas et al. 1972) was calculated as follows:

$$IRI = (N + W)F.$$

Food habit data were compiled separately for all individuals (N = 67), and for individuals ≤ 20 mm SL (N = 29), and for individuals 20–77 mm SL (N = 38), since the most noticeable shift in diet occurred at approximately 20 mm SL.

Differences in the distribution of YOY halibut among the three types of habitats (locations) in the Alamos Bay area were analyzed using Friedman's non-parametric method for randomized blocks (Sokal and Rohlf 1969). Data from 1984 beam trawls and from 1985 otter trawls were analyzed separately.

A comparison of recruitment success between the three years of the study was based on replicate small seine hauls collected from the shore within Alamos Bay. Catch-per-unit-effort (CPUE) for each sampling date within each year was

Table 1. YOY halibut mean length and growth rates for four comparable dates in 1983, 1984, and 1985 in Alamitos Bay.

Year	Date	$\bar{x}$ length (mm)	± 2 S.E.	N YOY halibut	$\bar{x}$ growth rate (mm/month)	$\bar{x}$ growth rate (mm/month)
1983	4 May	21.30	6.82	31		
	17 May	19.67	3.47	36	—	
	1 June	21.26	1.64	53	3.18	
	14 June	29.17	3.63	47	18.25	10.71
1984	12 April	21.48	3.05	23		
	15 May	30.32	7.45	17	8.04	
	6 June	44.86	8.97	14	18.97	
	20 June	62.33	5.93	2	37.44	21.48
1985	10 April	19.75	6.31	18		
	15 May	19.20	11.37	4	—	
	29 May	26.50	11.58	16	15.64	
	12 June	47.00	17.01	3	43.93	29.78

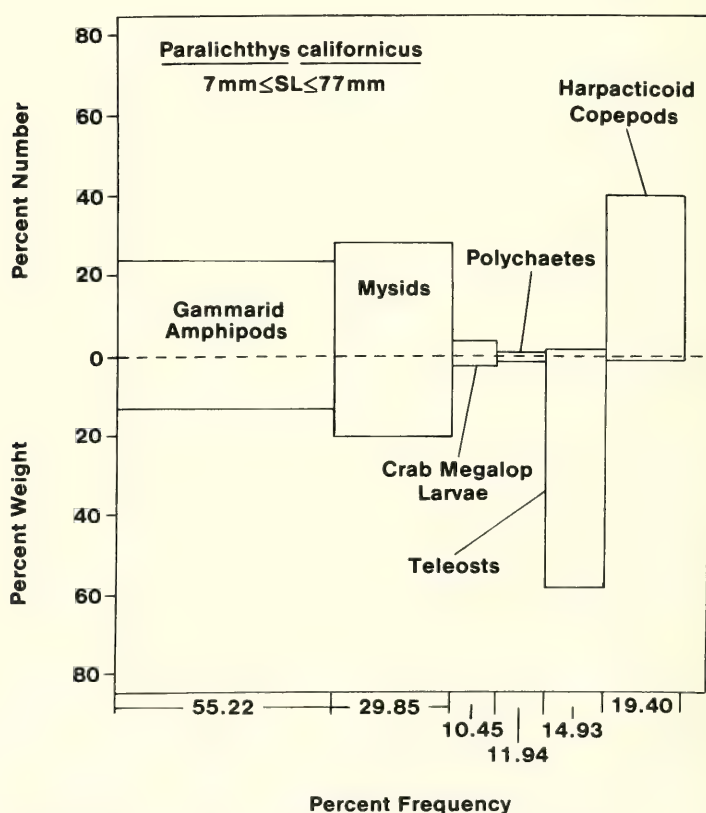


Fig. 3. Major food items occurring in the guts of YOY halibut from 7 mm to 77 mm in length. The area of each rectangle is proportional to the overall importance of a food item in the diet (IRI).

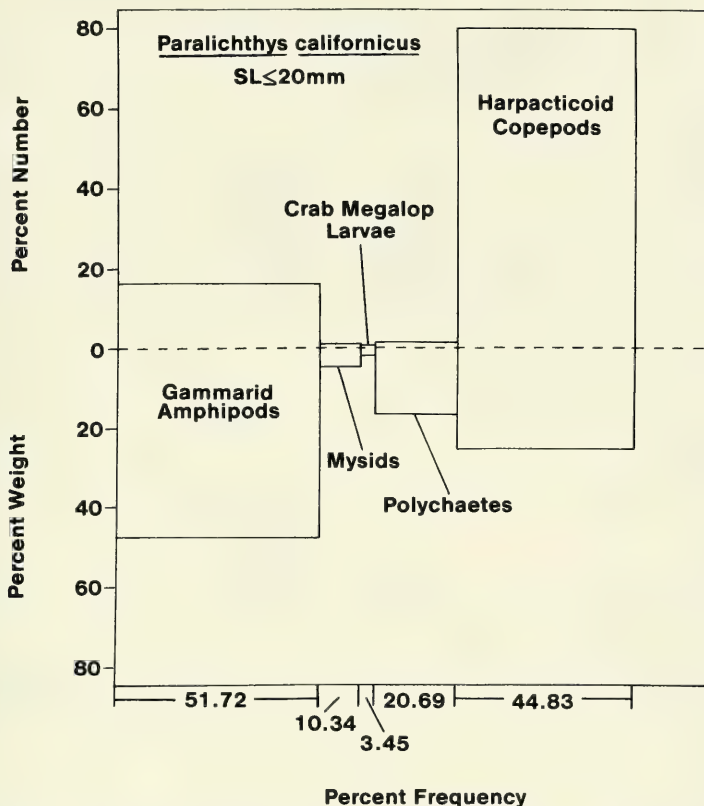


Fig. 4. Major food items occurring in the guts of YOY halibut <20 mm SL.

compared using the non-parametric Kruskal-Wallis test for differences of location in ranked data (Sokal and Rohlf 1969).

Parametric analyses were not carried out since the data were not normally distributed. Catch data in all cases were heavily skewed to the right due to zero catches. In addition, variances among the factor levels were consistently heteroscedastic. Neither various transformations nor combinations of replicates could overcome these problems.

Results

Length Frequencies

Young-of-the-year halibut ranged from 7–77 mm SL (the age-class cut-off). The vast majority of new recruits ranged between 8 and 12 mm SL. These individuals were generally clear with some visible melanophores indicating that they had only recently metamorphosed from the plankton. The smallest specimen collected (7 mm SL) had its upper eye partially migrated to the eyed-side. Eye migration was completed in all other new recruits.

Length frequency data from four comparable dates in each of the three years (Fig. 2) indicate that recruitment was strong and relatively continuous in 1983 with evidence of a persistent year class. In 1984, the recruitment was more sporadic

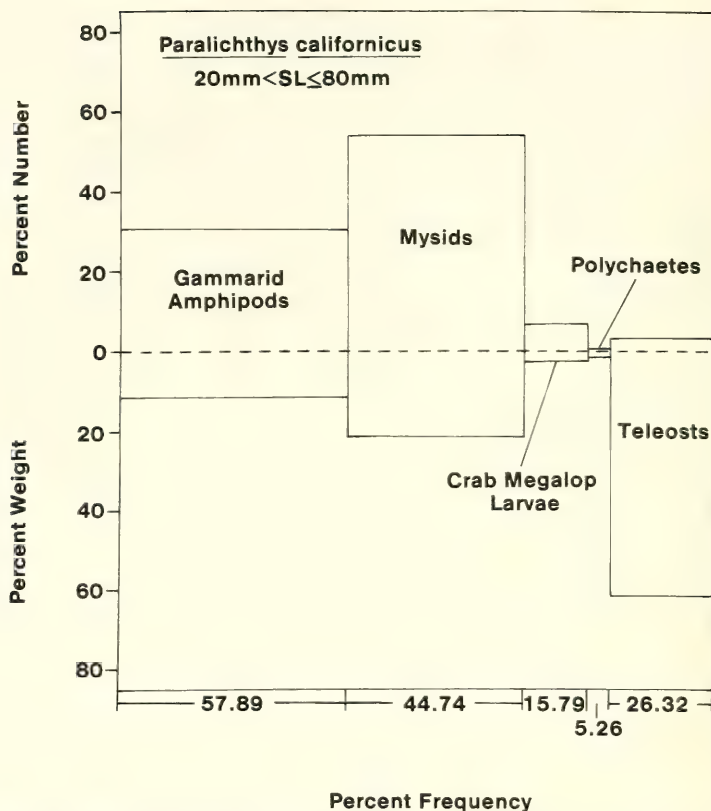


Fig. 5. Major food items occurring in the guts of YOY halibut between 20 mm SL and 80 mm SL.

with relatively high CPUE at times. An identifiable, persistent year class was not apparent in 1984. The recruitment and occurrence of YOY halibut in the nearshore areas was very light and sporadic throughout the 1985 sampling period. In each of the three years, there is some indication of multiple modes in length frequency. This is particularly evident in 1984 and 1985.

Estimated Growth Rates

Grand mean growth rates (mm/month) for each year ranged from 10.71 (1983) to 29.78 (1985) (Table 1) based on mean lengths of YOY halibut per sampling date. The values for 1983 are the most reliable since the size class was strongest and most persistent during that year. The sporadic nature of recruitment in 1984 and 1985 makes growth estimates misleading and highly variable.

Preliminary Age Determination

Due to difficulty in reading the sagittae, age analysis was limited to 10 individuals between 14 and 45 mm SL. The otoliths of specimens greater than 50 mm SL were too thick to be read accurately by transmitted light. The age-length relationship from these 10 individuals can be described by the linear equation $Y = 0.45x - 2.7$ ($r = 0.947$; $P < 0.01$) where Y is the standard length (mm SL)

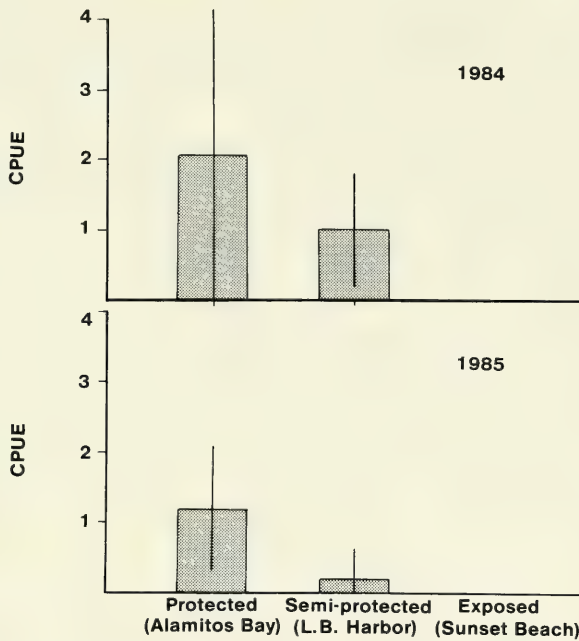


Fig. 6. Catch-per-unit-effort (no./tow) of YOY halibut among the three types of habitats (stations) in both 1984 and 1985 in the Alamitos Bay area. Error bars denote ± 2 S.E. CPUE is based on beam trawl samples in 1984 and on otter trawl samples in 1985.

and x is the number of growth rings. Based on this preliminary analysis, the smallest individual examined (14 mm SL) was approximately 42 days old. The largest (45 mm SL) was about 100 days old. Assuming linearity, we predict that new recruits at 8–12 mm SL are between 20 and 29 days old.

Stomach Content Analysis

The diet of all YOY halibut (7 mm–77 mm SL) was dominated by gammarid amphipods (IRI = 2027), mysids (1436), teleost fishes (901), and harpacticoid copepods (801) (Fig. 3). The diet of individuals 20 mm SL or less (Fig. 4) was dominated by harpacticoids (IRI = 4724), small gammarid amphipods (3300), and polychaetes (369). The dominant items in halibut between 20 mm and 80 mm SL (Fig. 5) were mysids (IRI = 3387), larger gammarid amphipods (2448), and teleosts (1703). Teleosts dominated the diet by weight (61.8% dry weight) and were found primarily in the stomachs of larger (>50 mm SL) YOY halibut.

Distribution Among Locations

The general patterns of distribution for 1984 and 1985 were virtually identical in the Alamitos Bay area, although the location difference in 1984 was not statistically significant ($\chi^2[2] = 3.17$; $P \sim 0.22$) due to low sample size, but was significant in 1985 ($\chi^2[2] = 8.36$; $P < 0.05$). Comparison sampling in 1984 near San Onofre-Oceanside yielded a nearly identical pattern of distribution between the three locations (protected, Aqua Hedionda, CPUE = 2.3; semi-protected, Oceanside Harbor, CPUE = 0.4, and exposed, five open coast stations, CPUE =

0.04). The greatest concentration of YOY halibut in the Alamitos area occurred in fully protected waters (CPUE of 2.1 in 1984 and 1.2 in 1985) (Fig. 6). The semi-protected habitat contained between one-half and one-quarter the concentration of YOY halibut. Recruitment of halibut was not observed in the exposed, open coast habitat off Sunset Beach. In 75 trawls taken in the exposed, open coast stations in both the Alamitos and San Onofre-Oceanside areas, only one YOY halibut (35 mm SL) has been captured in the 3 to 6 m depth range. No new recruits were ever collected in these exposed areas.

Recruitment Success

As indicated by the length frequency plots (Fig. 2), recruitment success varied greatly in the three years of the study based on small seine data from Alamitos Bay. Seine CPUE (± 2 S.E.) was highest in 1983 (4.6 ± 1.6) followed by 1984 (3.1 ± 3.4) and 1985 (0.1 ± 0.1). A comparison among the three years showed these differences in CPUE to be highly significant $\chi^2[2] = 11.83$; $P < 0.005$).

Discussion

Feeding Habits

Young-of-the-year halibut exhibited a marked ontogenetic shift in diet. Recently recruited (< 20 mm SL) halibut fed mainly on small, substrate-oriented prey such as harpacticoid copepods and small gammarid amphipods. YOY halibut larger than about 20 mm SL appeared to shift to larger prey items which are probably less substrate oriented, including mysids, teleosts (principally gobies), and larger gammarid amphipods. As YOY halibut within Alamitos Bay get larger, teleost fishes become more and more important to their diet.

Haaker (1975) found a similar pattern of dietary shift in young halibut from Anaheim Bay although the smallest halibut he examined were in the 40–50 mm SL range. Young halibut in Anaheim Bay shifted ontogenetically from small crustaceans and gobies initially to an almost exclusively piscivorous diet in older specimens. Plummer et al. (1983) examined the stomach contents of 336 California halibut (109 to 689 mm SL) trawled from 6 to 30 m depths off San Onofre and near Oceanside. The gut contents were dominated by northern anchovies (*Engraulis mordax*) and large mysids (notably *Neomysis kadiakensis*). Smaller halibut (< 250 mm SL) mainly contained mysids. Larger individuals (> 300 mm SL) mainly contained northern anchovy and other juvenile and adult fishes. It seems clear that halibut from most habitats exhibit a shift in diet according to size. They feed first (< 100 mm SL) on small benthic crustaceans, and as they increase in size, larger prey are incorporated into their diet. Large mysids and small fishes become increasingly important in the diet of medium (100–300 mm SL) size fish. Finally, larger fishes are the almost exclusive prey of larger halibut (> 300 mm SL).

Halibut occurring in bays probably encounter a different range of prey items in different abundances than those in nearshore areas. Haaker (1975) found gobies to be important food items from YOY halibut in Anaheim Bay. However, Plummer et al. (1983) determined that mysids were important in the diet of juvenile halibut from coastal waters. From the present study, it was evident that YOY halibut of equivalent size were feeding on different prey items in Alamitos Bay

as compared to YOY in Long Beach Harbor. YOY halibut within Alamitos Bay contained mainly harpacticoids, gammarids, and gobies, while those of comparable size in Long Beach Harbor contained mostly mysids which were abundant in the area.

Recruitment and Distribution

Halibut were recruited at sizes ranging from 8 to 12 mm SL in the Alamitos Bay area. This corresponds to an age of between 20 and 29 days based on the preliminary age-length relationship determined by examination of otoliths. If this aging is accurate, the planktonic larval period of halibut is, therefore, somewhere in the realm of 20 to 29 days after hatching.

No significant correlation between water temperature and the appearance of new recruits was evident in any of the three years of the study. In 1985, new recruits were sampled at temperatures ranging from 16.4°C to 22.9°C. Recruitment was sporadic and appeared to be independent of temperature in the nursery areas, at least in 1985. Water temperatures during the sampling times varied little in both 1983 (18.3–19.5°C) and 1984 (19.2–21.9°C).

This study has provided the first direct evidence in support of the view set forth by Plummer et al. (1983), that young-of-the-year California halibut occupy "embayments" almost exclusively. The results of the present study clearly show that in the area of Alamitos Bay YOY halibut recruit successfully to and are found only in protected or semi-protected waters. Concentrations of YOY halibut are greatest in the protected water within Alamitos Bay. This pattern may be consistent for the entire Southern California Bight since an almost identical pattern of distribution for YOY halibut was found independently in the San Onofre-Oceanside area further south in southern California.

A model of YOY halibut distribution based on these findings states that "recruitment of halibut will occur anywhere that there are relatively calm waters (protected or semi-protected) and these areas will be nursery areas for the young-of-the-year halibut." Calm waters might include not only bays/estuaries and harbors, but also the leeward sides of points and islands. This general, verbal model allows predictions to be made of where YOY halibut should recruit and occur. These predictions can be tested by sampling for YOY halibut with appropriate gear in areas in question at the correct time of year.

The variable recruitment success of YOY halibut among the three years in the study area is intriguing but, as yet, cannot be explained. The most successful recruitment of the three years based on CPUE was 1983, followed by 1984 with a sporadic, "medium" recruitment, and by 1985 with a sporadic, light recruitment. A few of the many possible explanations include: 1) general oceanographic conditions off the Alamitos Bay area were very different in the three years, 2) productivity within this nearshore area possibly varied, 3) the El Nino event of 1982–1983 had some effect on halibut populations, 4) stronger net transport upcoast in 1983 may have brought more potential recruits into the area from southern waters, and 5) fishing pressure on spawning adults offshore of general Alamitos Bay area in the form of gill-netting may have had an effect over the last three years. Whatever the reason, it is clear that some event or events strongly influenced the recruitment success and/or the larval survivorship in the Alamitos Bay-Long Beach Harbor area for the three years, 1983–1985.

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Research Notes

Records of *Mugil curema* Valenciennes, the White Mullet, from Southern California

Mugil cephalus Linnaeus, the striped mullet, has a cosmopolitan tropical and warm-temperate distribution and is the only mugilid listed from Californian waters (Eschmeyer, Herald and Hammann 1983; Fitch and Lavenberg 1971; Hubbs, Follett and Dempster 1979; Miller and Lea 1972, 1976). Striped mullet are relatively common in estuaries and lagoons south of Pt. Conception and occasionally range as far north as San Francisco Bay (Reilly and Sakanari 1982). They were once abundant in the Salton Sea and remain a common fish in the lower Colorado River where they are utilized as a food fish (Minckley 1973; Moyle 1976). White mullet, *Mugil curema*, are similar to striped mullet in that they occur in tropical shelf waters shallower than 200 meters over sand and mud substrata, at times in brackish and freshwater, but are unknown north of Magdalena Bay on the outer coast of Baja California. *Mugil curema* occurs in both the tropical Pacific and Atlantic off the Americas. In recent years marine biologists and fishermen have suspected that a second species of mullet might occur in the bays and estuaries of southern California.

On 20 August 1982, 13 mullet were collected by beach seine in upper Newport Bay, Orange Co., by John Sunada of the California Department of Fish and Game (CDFG). On 11 May 1983, eight mullet were collected in Bolsa Bay, Orange Co., by Eric Knaggs also of the CDFG. Although both collections were initially identified as *Mugil cephalus*, they seemed atypical. These fish were turned over to the Natural History Museum of Los Angeles County (LACM). The Newport Bay fish are catalogued as LACM 44375-1; 13: 155-192 mm standard length (SL). Of the eight Bolsa Bay specimens, two were preserved (LACM 43461-1; 2: 226-238 mm SL) and six were skeletonized by maceration (LACM 43461-2 through 7; 6: 223-237 mm SL). The specimens from both collections were in extremely poor condition and their specific determination was not confirmed until the acquisition of a similar mullet from south San Diego Bay on 25 May 1985. We identified this specimen as *Mugil curema* Valenciennes, the white mullet, and recognized it as conspecific with the material from Newport and Bolsa bays. The San Diego Bay mullet (LACM 44108-1; 293 mm SL), was taken in a gill net set by Luigi Sanfilippo, a commercial mullet fisherman, who speculated it was not the striped mullet he usually caught. Additional white mullet have since been taken by Mr. Sanfilippo. A minor fishery exists for mullet in San Diego Bay where these fish are sold fresh primarily for local consumption. Landings from this fishery since 1980 have varied from 19,000 (1984) to 45,000 (1980) pounds per year.

Diagnostic characters that separate the various species of eastern Pacific Mugilidae have been presented by Ebeling (1957, 1961) and Chavez (1985). Superficially, striped mullet (=s) and white mullet (=w) are similar; however, the following characters distinguish them: dorsal profile and cross section of head—blunt and depressed (s) vs. wedge-shaped and more rounded (w) (Figure 1); soft

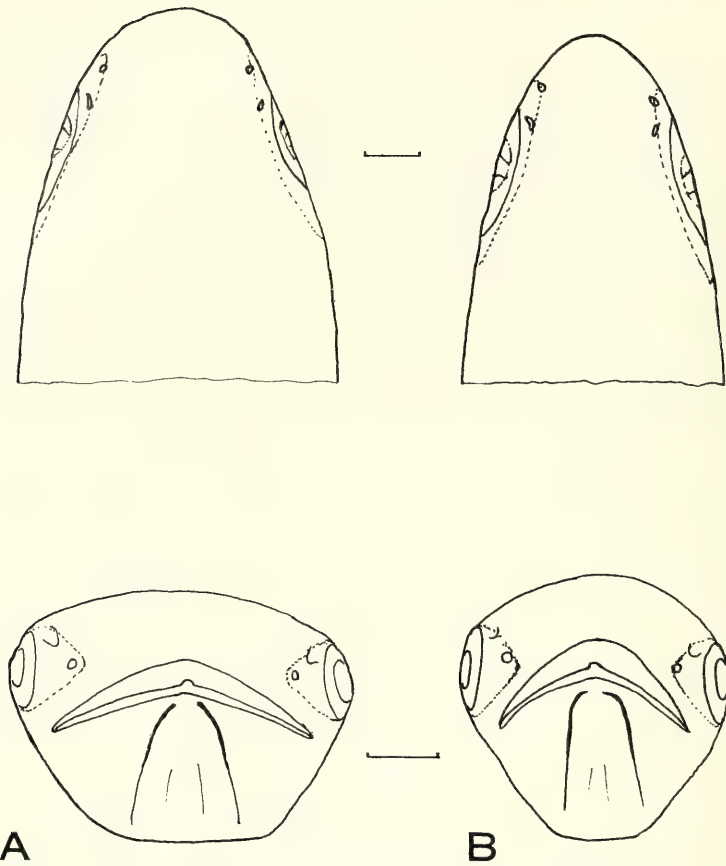


Fig. 1. Dorsal (upper) and anterior (lower) views of heads of: A. *Mugil cephalus* (LACM 44108-2; 322 mm SL), and B. *Mugil curema* (LACM 44108-1, 293 mm SL); both taken in San Diego Bay on 25 May 1983. The lower figures are based on a cross section of the head taken at rear margin of eyes to emphasize differences in head shape, which is not so striking where the head meets the body. Scales both equal one centimeter.

dorsal and anal fins—lacking scales (s) vs. densely scaled (w); tooth morphology—primary teeth simple and secondary teeth bifid (s) vs. all teeth simple (w); total anal fin elements—10 or 11 (s) vs. 12 or 13 (w); general body coloration—grey, distinctly striped (s) vs. silvery, faintly striped or unstriped (w). In addition, when fresh or observed alive underwater, white mullet have a yellower caudal fin, which has a blackened posterior margin that is lacking in striped mullet.

Selected counts and measurements (in mm) for the San Diego *Mugil curema* (LACM 44108-1) are: Dorsal fin IV + 8; anal fin III, 9; pectoral fin (left) 17; vertebrae 12 + 12 = 24; total length 371; head length 70.2; pectoral fin length 40.4; pectoral axillary scale 18.2; anal fin base 42.0; longest anal fin ray 34.0.

Two suppositions concerning the provenance of white mullet in California waters can be addressed. First, the capture of this species in 1982, 1983 and 1985, at the possible onset, during and immediately following the 1982–84 El Niño event may be directly related to the occurrence of warm water along Baja California and California. If so, *Mugil curema* might be expected to make its appearance off

California from those waters off southern Baja California and mainland Mexico only during anomalously warm-water periods, a pattern similar to round herring, *Etrumeus acuminatus*, and the southern subpopulation of Pacific sardine, *Sardinops sagax*, which made sudden appearances off southern California during the 1982–84 El Niño event (Lavenberg et al. 1986). In such cases occurrence could be associated with either movement of adults (responding to thermal gradients in the eastern Pacific (Simpson 1984a, b)) or to larval–prejuvenile transport. Larvae and juveniles of the genus *Mugil* are planktonic, primarily associated with neuston for a lengthy period (at least two months), and are common in the offshore waters of Baja California. Cowan (1985) has demonstrated that large scale variation in recruitment of sheephead, *Semicossyphus pulcher*, off California is consistent with annual oceanographic conditions. The early life history stages of sheephead are also planktonic and are subject to transport by currents. During the El Niño event of 1982–84 sheephead recruitment in southern California appeared to have been from southern populations (Cowan 1985). It seems to us that both means of transport are possible for *Mugil*, either as larval–prejuvenile dispersion or adult movement. These two modes are not necessarily mutually exclusive. Second, we do not discount the possibility that *M. curema* historically has been a component of the bay fauna of southern California and has remained undetected because of its similarity to *M. cephalus*.

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Digestion and Abnormal Expulsion of a Jackknife Clam *Tagelus subteres* by a Sandstar *Astropecten armatus*

Sandstars of the widespread genus *Astropecten*, living on and under intertidal and subtidal sandy bottoms, are important predators of shelled molluscs, both gastropods and bivalves, as well as other organisms. *Astropecten* spp. do not possess grasping suckers on their tube feet. They swallow their prey whole carrying out digestion internally (Hyman 1955). If the prey are bivalves *Astropecten* then expels either ungaped (undigested), partially or fully gaped animals through the oral opening. Clearly the degree of digestion and the size of the bivalve will influence the ease with which an *Astropecten* will eliminate its prey in the normal manner.

Prenant (1936) and Lems (1951) report that *Astropecten irregularis* are damaged by the swallowing of bivalves that became too large to handle after their valves gape following digestion of the soft tissues. Prenant collected an individual in which the pair of *Donax trunculus* valves were sticking symmetrically through the aboral wall of the sandstar with indications of regeneration of the aboral integument over the valve hinge. Lems found a number of *Astropecten* with worn spots on the aboral surface where valves of swallowed *Donax vitatus* pressed on the underside. In one individual the entire left valve and the dorsal portion of the right valve had punctured the aboral surface at an angle.

Christensen (1970) is fairly convinced that the phenomenon cannot occur in a living *Astropecten*. He maintains that previous reports were made on dead and, in most cases, dried specimens. He also invokes his own observations, suggesting that he did observe the phenomenon although he gives no details. He does offer a drawing of a specimen of *Astropecten irregularis*, sent to him by Engel from Holland, showing the edge of the right valve of a gaped *Donax vitatus* poking through the aboral surface. Engel assumes and Christensen concurs that fissures in body walls of *Astropecten* spp. which have engulfed and digested large bivalves are postmortal in origin and have come about when sandstars have been washed ashore, died and dried in the sun during low tide. The sharp edges of one or both valves then perforated the shrunken skin of the sandstar. While there is no way to determine whether Engel's specimen had a pre- or postmortal puncture, the photographs of Prenant's and Lem's specimens strongly suggest to me that abnormal expulsion of gaped bivalves was occurring while *Astropecten* was alive. Corroboration of this possibility follows from the following account.

I report an event in which one valve of a digested, fully gaped 46.5 mm long jackknife clam (*Tagelus subteres* [Conrad, 1873]) is ejected through the mouth of a 126 mm *Astropecten armatus* Gray, 1840 while the second valve is slowly forced through the stomach and aboral body wall. Since the valves gaped but remained hinged throughout the digestive process, they ultimately came to lie in a plane at right angles to the oral-aboral axis. The sandstar was unable to maneuver both valves through the oral opening; thus one was ejected orally and the other aborally while they were still hinged. Both valves were then forced through the side of the *Astropecten*, almost severing it in two. Over the following week the sandstar tore

itself into two parts, one with two arms and the madreporite, the other with three arms. The details are as follows:

On 27 February 1983, during low tide, an *Astropecten armatus* showing a large, aboral bulge outlining the long axis of a jackknife clam was collected in lower Newport Bay, Orange County, California and transferred to a circulating seawater system at California State University, Northridge.

Three days later I observed a cleaned valve of *T. subteres* partially protruding through the oral opening of *Astropecten*. On the following day the edge of the second valve broke through the aboral wall while the first valve was completely out of the mouth but held there by the hinge. By 3 March the opposite end of the second valve was also through the aboral surface; the middle of the valve being covered by the epidermis (Fig. 1a). *Astropecten* actively cruised around the tray and reburrowed rapidly when placed on the surface of the sand. On the morning of 5 March the second valve was pushed through the remaining strands of aboral epidermis. Over the next two days the cleaned pair of valves was maneuvered through the side of the sea star, partially cutting it into two; a two-armed section with madreporite and a three-armed section. The partially rendered *Astropecten* was active throughout the day. Periodically one or another arm would be raised putting a tearing force on the wound. During 8 and 9 March the two-armed section was forced under the three-armed section as a shearing force was applied along the wound line. This behavior continued for the next four days as the tissue bridge between the sections narrowed. On 14 March the sections separated (Fig. 1b).

Both sections of *Astropecten* remained active for the following month. During the middle of April the three-armed section died and disintegrated. The two-armed section regenerated slowly; three minute arms were present on 1 November. Shortly thereafter the animal died when the sea water system broke down.

Christensen and Engel notwithstanding, a living *Astropecten* may expel at least one valve of a gaped bivalve through its aboral surface. It is difficult to generalize about the phenomenon. While *Astropecten* spp. may occasionally swallow large bivalves, most prey appear to be small. Gemmell, Hertz, and Myers (1980) found mostly small bivalve prey in *A. armatus* from the Gulf of California as did Wells, Wells, and Gray (1961) in *A. articulatus* from North Carolina. Of 1051 *A. irregularis* examined by Christensen (1970) 95% of the bivalves were 2.9 mm long or less. However, he does mention an 80 mm long *A. irregularis* normally expelling a 25.3 mm *Macoma calcarea* and a 32 mm long *Cultellus pellucidus* inside an *A. irregularis* of unstated dimensions. Ribi, Schärer, and Ochsner (1977) found *A. aranciatus* ranging in size from 107 mm to 190 mm orally eliminating bivalves between 2 mm and 21 mm in length while *A. hispidus* between 65 mm and 103 mm were similarly occupied with bivalves between 1 mm and 19 mm. In another study *A. aranciatus* averaging 152 mm expelled bivalve prey from 1 mm to 30 mm long with the majority measuring 10 mm or less (Ribi and Jost 1978). While Lems (1951) gives no measurements for his aborally protruded bivalve, Prenant (1936) does; the sandstar was 86 mm long and the clam 33 mm long.

Where measurements permit, including the specimen sent to Christensen by Engel, I have calculated the length to length ratios of *Astropecten* and engulfed bivalves. Where aboral expulsion has occurred *Astropecten* is $2.7\times$ or less the length of the bivalve. Where aboral expulsion is not indicated *Astropecten* is $3.1\times$ or more the length of the bivalve. Whether a critical size relationship determines

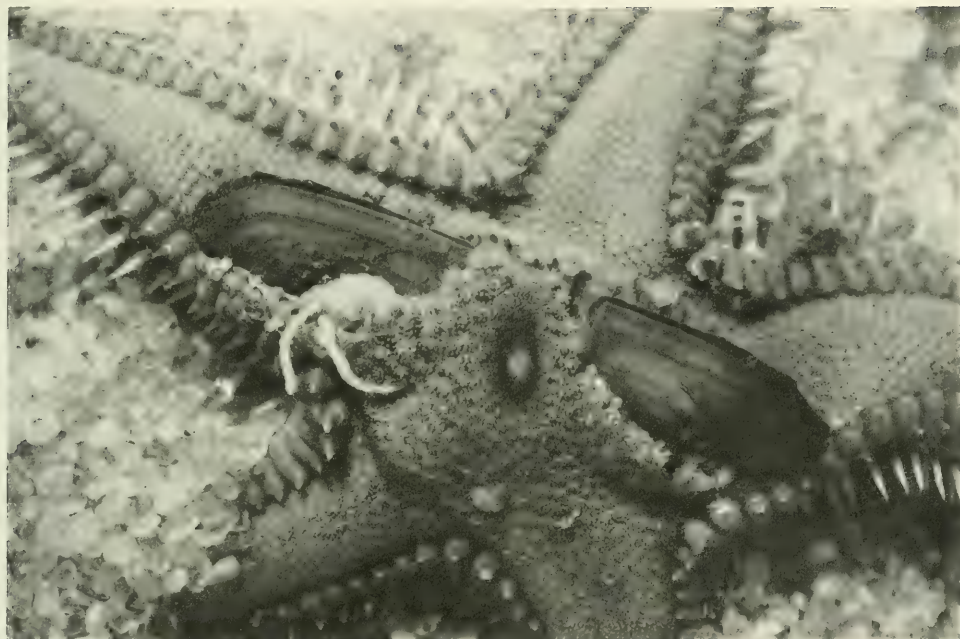


Fig. 1a. Aboral view of *Astropecten armatus* with both ends of one valve of *Tagelus subteres* protruding through the aboral epidermis.



Fig. 1b. Aboral view of *Astropecten armatus* after separation of two and three-armed section. Madreporite (light circular area) visible in two armed section. Photographs reproduced from 35 mm Kodachrome slides.

the incidence of abnormal expulsion will require additional measurements from natural events or from deliberate feeding experiments with large bivalves.

This report is the first known of an *Astropecten* tearing itself into two parts in the process of expelling an unusually large, gaped bivalve. Regeneration of the disk and three arms on the madreporite bearing two-armed section was underway while the three-armed section disintegrated prior to the system breakdown and the death of the sandstar. In the field I have occasionally observed *A. armatus* with one or two partially regenerating arms but never with a regenerating disk. However, disintegrating sandstars, either whole or in part, are not uncommon. Whether one can extrapolate from an event in the laboratory under relatively controlled, benign conditions to the field under natural, highly variable conditions is debatable at this time.

Addendum

On December 2, 1986, during low tide at the same location in lower Newport Bay, I collected a second living *Astropecten armatus* with both valves of a fully digested, gaped *Tagelus subteres* protruding through the aboral body wall while a short section of the left valve protruded through the mouth. The animal was established in a sea water tray in my laboratory and by December 8 had ejected both valves partially tearing itself into two parts. Its progress is being followed.

Since the sandstar measures 120 mm through the longest arms and the jackknife clam 49.5 mm through its long axis, the length to length ratio is 2.4 and falls under the 2.7 ratio calculated above.

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Abundance of Harbor Seals on San Miguel Island, California, 1927 through 1986

Harbor seals (*Phoca vitulina richardsi*; Shaughnessy and Fay 1977) haul out on all of the Southern California Channel Islands and breed at each with the possible exception of Santa Barbara Island (Stewart et al. *in press*). The number of seals observed on San Miguel Island (34°02'N, 120°22'W) has been, in general, consistently larger than that at any of the other islands (Stewart et al. *in press*). There seals haul out primarily on four sandy beaches on the north coast and three on the south coast (Stewart 1981a). The number of seals ashore varies during the day (peak numbers are ashore in early afternoon; Stewart 1981a, 1984) and the year (peak numbers are ashore in late May to early June, when seals are molting; Stewart 1981a, b; Stewart and Yochem 1984). Births occur from mid-February through mid-April, although most are in March, and nearly all pups are weaned by early May (Stewart 1981b).

Bonnot (1928:30) observed three harbor seals on San Miguel Island in summer 1928. The few published data since then (i.e., Bartholomew and Boolootian 1960; Carlisle and Aplin 1966; Frey and Aplin 1970; Odell 1971) suggest they were uncommon on the Southern California Channel Islands prior to the 1970's (Stewart et al. *in press*).

We report here our counts of harbor seals on San Miguel Island in late spring from 1973 through 1983 and use them to examine recent trends in abundance. Since individual seals do not haul out every day and because all seals are rarely, if ever, ashore simultaneously (Stewart and Yochem 1983; Yochem and Stewart 1985), the counts reported are minimal estimates of population size. However, we estimate absolute abundance using corrections derived from radiotelemetry studies (Stewart and Yochem 1983) and discuss the reliability of those estimates.

Methods

We made aerial surveys each year from 1973 through 1983, and in 1985 and 1986 in late May and early June between 1200 hr and 1500 hr when the greatest number of seals was expected to be hauled out (Stewart 1981b, 1984; Yochem and Stewart 1985). We made those surveys in a single or twin engine, high wing aircraft at altitudes between 150 m and 250 m and photographed seals with a 35 mm camera (hand held) and a 200 mm lens. Counts of seals were later made from black and white enlargements or from projected color imagery.

We calculated observed instantaneous rates of increase ($\bar{r}$) using the regression method (ln number of seals regressed on time, where $\bar{r}$ is the slope of the regression line; Caughley and Birch 1971; Caughley 1977; McCullough 1982) and converted those exponential rates to finite rates ($\lambda = e^{\bar{r}}$), which are more appropriate for "birth-pulse" species (Caughley 1977:6; Eberhardt 1985) such as harbor seals.

We estimated absolute abundance (X) and 95% confidence intervals as follows:

$$X = N/A;$$

$$95\% \text{ confidence interval} = N/[A + (S.E.)(1.96)]$$

where:

N = the number of seals counted,

A = average proportion hauled out during survey (= .64);

S.E. = standard error of A (= .06);

and A and S.E. are from Stewart and Yochem (1983).

Results and Discussion

The annual increase in seals hauled out in late spring averaged about 22% from 1958 (when the first systematic surveys were made) through 1976 ($\bar{r} = .20$, $R = .91$; Fig. 1). Such a high rate of increase is uncommon among large mammals though there are a few well documented cases (e.g., Antarctic fur seals—Payne 1977; white-tailed deer—McCullough 1982; feral horses—Eberhardt et al. 1982; northern elephant seals—Cooper and Stewart 1983). Some pinniped populations increased rapidly on the Channel Islands and elsewhere after commercial harvests and bountied killings ended in the 1800's and 1900's (e.g., California sea lions and northern elephant seals—Stewart et al. *in press*; harbor seals—Scheffer 1928; Pearson and Verts 1970; Newby 1973; Brown and Mate 1983; Payne and Schneider 1984). Although harbor seals were occasionally killed on the Channel Islands during the early 1900's (e.g., Cockerell 1938), they were never harvested or bountied to any extent. Their rapid increase in abundance in the 1960's and 1970's on San Miguel Island, and other Channel Islands (Stewart et al. *in press*) which are near the southern limit of the species' range, may have resulted from relatively high immigration from recovering populations further north. We believe it unlikely, however, that rates of population increase in northern regions were high enough to sustain sufficiently high emigration to account for the increases in Southern California. Alternatively, combinations of high fecundity and low mortality of seals in Southern California during that period would have been required to account for the increases observed. Data are not available, however, to test those hypotheses.

Harbor seal numbers continued to increase from 1976 through 1986 ($\bar{r} = .05$, $R = .75$) but much slower than previously, perhaps because of density-dependent influences on vital rates, entanglement and mortality of seals in fishing gear and marine debris (Stewart and Yochem 1985a, 1987) or changes in haul-out patterns acting singly or in combination. Mortality of seals in drift and set gill net fisheries has apparently increased recently in coastal waters of California (e.g., Hanan et al. 1986). The impacts of those mortalities on harbor seal abundance on the Channel Islands are, however, unpredictable.

We estimated that there were about 1830 harbor seals in the San Miguel Island herd in 1987 (Fig. 1) but because the age and sex composition of seals ashore may vary seasonally (Yochem and Stewart 1987), this is probably an underestimate. In addition, the accuracy of an estimate of absolute abundance (Fig. 1) is dependent on the consistency among years of the average proportion of seals hauled out and on the similarities of haul-out patterns on San Nicolas (where correction factors were derived) and San Miguel islands. Interpretations of recent trends in abundance based on counts are also sensitive to those influences, but there are few data available to examine temporal and geographic variability of

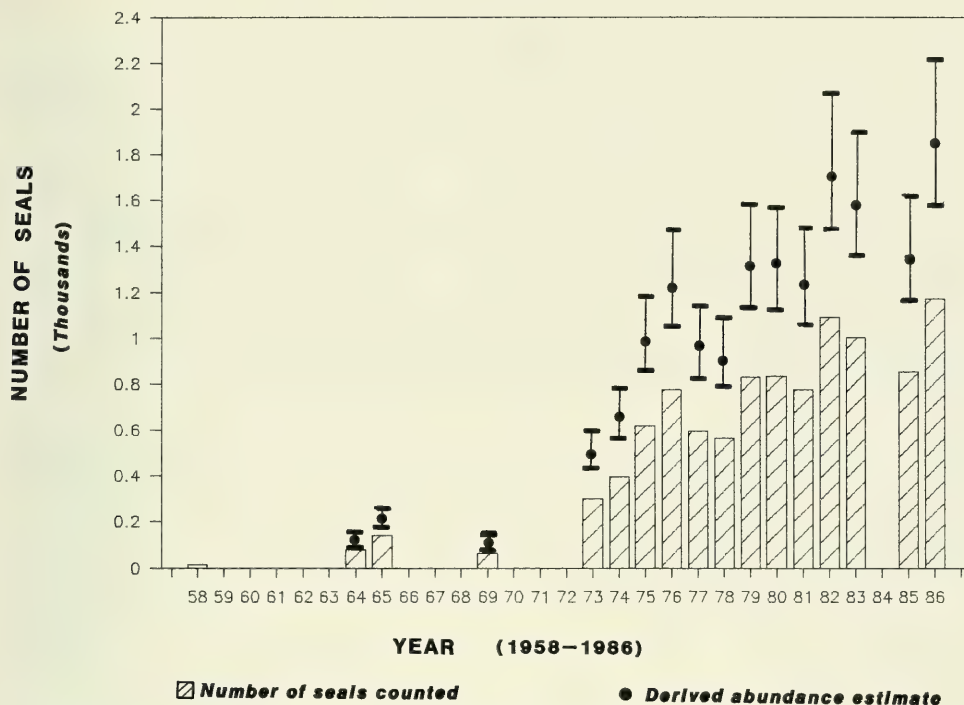


Fig. 1. Annual peak counts and estimated absolute abundance (with 95% confidence intervals) of harbor seals on San Miguel Island, 1958-1986.

haul-out patterns. On San Nicolas Island, the proportions of radio-tagged seals hauled out in afternoon in late May and early June were much smaller in 1983 than in 1982 (Yochem and Stewart 1985). Those differences may be related to differences in age and sex compositions of seals tagged in 1982 and 1983 or to the influence of the 1982/1983 El Niño Southern Oscillation event on seals' behavior as evidenced by changes in their diet at San Nicolas Island in 1983 (Stewart and Yochem 1985b), or both.

Accurate determinations of absolute abundance of harbor seals on the Channel Islands and elsewhere will require further studies of temporal, geographic, and habitat influences on the proportions of seals ashore.

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Pacific White-sided Dolphins (*Lagenorhynchus obliquidens*) in the Sea of Cortez

Leatherwood et al. (1984) reviewed data on distribution and movements of Pacific white-sided dolphins, *Lagenorhynchus obliquidens*, in the eastern North Pacific (east of 180 degrees west longitude). The 1300 records they judged reliable, documented the occurrence of this species in coastal, continental shelf, and pelagic waters and from about 20 degrees to 61 degrees north latitude; the most northerly record, from Valdez, Alaska, in Prince William Sound, and the most southerly, from Islas Revillagigedos, Mexico, were considered extralimital. It was concluded that in the eastern North Pacific this species is primarily an inhabitant of temperate waters between about 23 degrees north latitude and the southern Alaskan coast. It undertakes pronounced movements north-south and inshore-offshore in various areas and seasons.

There are only a handful of verified records of white-sided dolphins from the southern Baja California peninsula (Leatherwood et al. 1984: fig. 7). Of those, the only ones indicating presence of this dolphin species in the Gulf of California (Sea of Cortez) are fishermen's accounts from the 1960's and early 1970's of occasional sightings near Gorda Bank, in the mouth of the Gulf (Leatherwood et al. 1982). Heretofore, there has been no information indicating penetration very far into the Sea of Cortez.

Table 1. Recent sightings of Pacific white-sided dolphins in the southwestern Sea of Cortez.

Date	Location	Number of individuals	Observations
23 June 1981	Canal de San Lorenzo 24°23'N, 110°20'W	ca. 25	Seen 250 m from R.V. Ellen B. Scripps.
25 April 1982	Canal de San Lorenzo	ca. 100	Feeding in company of an adult California sea lion, <i>Zalophus</i> sp., identified by divers at <6 m distance.
28 April 1982	Canal de San Lorenzo	8-9	
19 June 1982	Canal de San Lorenzo	ca. 150	
31 March 1983	Near Cabo San Lucas 22°45'N, 109°50'W	3	M. Webber, M.V. Executive; small animals.
15 April 1984	Canal de San Lorenzo	ca. 200	Group included newborn calves.
20 February 1985	Between Isla Cerralvo and Baja California 24°15'N, 110°05'W	5	K. Connally S/R/V Diamaresa (see Connally et al. 1985).
23 February 1985	West of Isla Espiritu Santo 24°30'N, 110°25'W	2	K. Connally S/R/V Diamaresa (see Connally et al. 1985).
6 March 1985	Near Isla Danzante 25°50'N, 111°00'W	15	S. Leatherwood, R/V Sea World.

Between June 1981 and March 1985, we and colleagues encountered white-sided dolphins on nine occasions between about Punta Gorda and Isla Danzante, in the southwestern Sea of Cortez (Table 1). The sightings were logged incidental to tourist activities or other research, so were not investigated in detail. All occurred between spring and early summer, part of the period (winter through spring) when the greatest number and variety of cetaceans appear to congregate in the Bay of La Paz (Auriolos and Muñoz, unpublished data). "Groups" contained 2 to over 250 individuals and were all over the narrow shelf separating the peninsula shores from the adjacent pelagic zone. Two groups (on 20 and 23 February 1985) were associated with the common dolphin, *Delphinus delphis*, a common association elsewhere. These two species are sympatric. Collectively, these records suggest that white-sided dolphins are not infrequent visitors, at least seasonally, to waters of the southwestern Sea of Cortez.

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***Detonella papillicornis* (Richardson)**
(Isopoda: Oniscidea: Scyphacidae)
from Bolinas Lagoon, California

Even though it has an extensive range, *Detonella papillicornis* (Richardson) has been only sporadically collected. The species was originally described by Richardson (1904) on the basis of a single male (Schultz 1972) from Seldovia, Alaska. Fee (1926) collected an additional specimen of *D. papillicornis* at Hammond Bay in British Columbia, Canada. Lohmander (1927) reported and described four individuals from Bering Island, Russia, which were collected in 1897, and Hatch (1947) reported *D. papillicornis* from Ketchikan, Alaska, and Friday Harbor, Washington. See Van Name (1936) for a discussion of the species and early synonymy.

Unfortunately, Richardson's description of *Detonella papillicornis* was inaccurate in several respects (Lohmander 1927; Schultz 1972) and her figures were, as Lohmander put it, somewhat schematic, making it unlikely that new collections of *D. papillicornis* could have been recognized as such on the basis of Richardson's description alone. This situation is evidenced by the fact that Verhoeff, on the basis of Richardson's and Lohmander's descriptions, erected a new species (*Detonella lohmanderi* Verhoeff) for Lohmander's specimens, and suggested that *D. papillicornis* and *D. lohmanderi* probably belonged to different families (Verhoeff 1942). However, for the reasons put forth by Hatch (1947), and with the redescription of Richardson's type specimen by Schultz (1972), and considering the fact that Richardson herself identified the Bering Island specimens (Lohmander 1927), there is no doubt that *D. lohmanderi* is a junior synonym of *D. papillicornis*. With Lohmander's (1927) excellent description and illustration of *D. papillicornis*, and Schultz's illustration of the whole animal (Schultz 1972), *D. papillicornis* is now adequately described and figured and easily recognizable.

I collected a single female specimen of *Detonella papillicornis* (5 mm long) at Bolinas Lagoon in Marin County, California, on 30 May 1986, and an additional six specimens (3 females, lengths = 3.25, 3.00, and 2.50 mm; 2 males, lengths = 3.75 and 2.00 mm; and 1 juvenile, length = 1.25 mm) at the same site on 27 September 1986. None of the females was gravid. The female collected on 30 May had a distinctly orange colored body with reddish-orange eyes. The remaining specimens possessed black eyes and light brown body color as described by Richardson (1904). All specimens were collected at the southern end of the lagoon at the high tide line. Specimens were found under rocks and gravel in grass and pickleweed. Other oniscids found at the site were *Mauritaniscus littorinus* (Miller), *Armadilloniscus coronacapitalis* Menzies, *Armadilloniscus lindahli* (Richardson), *Armadillidium vulgare* (Latreille), and *Porcellio scaber* Latreille.

The "red eyed/red body" color morph of the specimen collected on 30 May is not uncommon in oniscids and has been previously reported in *Armadillidium vulgare* (Vandel 1945), *Venezillo evergladensis* Schultz (Johnson 1976), *Porcellio scaber* (Schultz et al. 1982), *Porcellio dilatatus* Brandt & Ratzeburg (Sassaman

and Garthwaite 1980), and *Mauritaniscus littorinus* (Schultz et al. 1982). I have also observed this color morph in *Trachelipus rathkei* (Brandt).

Lohmander (1927) considered *Detonella papillicornis* to have a subarctic distribution. The collection of *D. papillicornis* from Bolinas lagoon in central California, which extends the range of this species 1150 km to the south, is clearly outside of the subarctic region. The oniscids of California have never been adequately collected, and accurate historical information on the species present in California and their distributions does not exist. It is thus impossible to say whether this southern collection represents a recent introduction of *D. papillicornis* into California or a natural part of the range of this species.

Two individuals of *Detonella papillicornis* from Bolinas Lagoon have been deposited in the Santa Barbara Museum of Natural History (SBMNH 34871) and an additional two specimens have been deposited in the National Museum of Natural History (USNM 233301). I thank Floria Parker for help in collecting the specimens.

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McWilliams, K. L. 1970. Insect mimicry. Academic Press, vii + 326 pp.

Holmes, T. Jr., and S. Speak. 1971. Reproductive biology of *Myotis lucifugus*. J. Mamm., 54:452–458.

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COVER: *Dendraster excentricus*, a dominant sand dollar species of the subtidal sand community of the exposed coast of Southern California. Photograph submitted by authors, Morin, Kastendiek, Harrington and Davis. Page 1.